Estructura, dinámica y regeneración de los bosques mixtos de alcornoque (*Quercus suber* L.) y quejigo moruno (*Quercus canariensis* Willd.) del sur de la Península Ibérica: una aproximación multiescala

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T. Itziar Rodríguez Urbieta
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Tesis Doctoral

Universidad de Alcalá
Departamento de Ecología

UNIVERSIDAD DE ALCALÁ
DEPARTAMENTO DE ECOLOGÍA

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Memoria presentada para optar al grado de
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T. Itziar Rodríguez Urbieta

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HACEN CONSTAR:

Que el trabajo descrito en la presente memoria, titulado **"Estructura, dinámica y regeneración de los bosques mixtos de alcornoque (*Quercus suber* L.) y quejigo moruno (*Quercus canariensis* Willd.) del sur de la Península Ibérica: una aproximación multiescala"**, ha sido realizado bajo su dirección por Dña. T. Itziar Rodríguez Urbieta en el Departamento de Ecología de la Universidad de Alcalá y en el Instituto de Recursos Naturales y Agrobiología de Sevilla, CSIC, y reúne todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Alcalá de Henares, a 14 de abril de dos mil ocho,

Dr. Miguel Ángel Zavala Gironés

Dr. Teodoro Marañón Arana

Universidad de Alcalá

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Miguel Ángel Rodríguez Fernández, Profesor Titular de Ecología de la Universidad de Alcalá y Director del Departamento de Ecología,

HACE CONSTAR:

Que el trabajo descrito en la presente memoria, titulado **"Estructura, dinámica y regeneración de los bosques mixtos de alcornoque (*Quercus suber* L.) y quejigo moruno (*Quercus canariensis* Willd.) del sur de la Península Ibérica: una aproximación multiescala"**, ha sido realizado por Dña. T. Itziar Rodríguez Urbieta dentro del Programa de Doctorado Cambio Global y Desarrollo Sostenible adscrita al Departamento de Ecología de la Universidad de Alcalá, y reúne todos los requisitos necesarios para su aprobación como Tesis Doctoral.

Alcalá de Henares, a 14 de abril de dos mil ocho,

Dr. Miguel Ángel Rodríguez Fernández

A mis aitatxos,

Mariasun y Clemente

The old idea of a static landscape, like a single musical chord sounded forever, must be abandoned, for such a landscape never existed except in our imagination. Nature undisturbed by human influence seems more like a symphony whose harmonies arise from variation and change over every interval of time

D.B. Botkin

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En mi primera etapa en Bélgica realicé los cursos de doctorado como estudiante erasmus (después de convencer al personal de Tercer Ciclo de la Universidad de Salamanca a la que entonces pertenecía). Empezó a picarme el gusanillo por la investigación gracias al profesor Bart Muys y a Tim Wagendorp de la Universidad KULeuven, que me dieron la oportunidad de colaborar en su proyecto y de asistir a mi primer congreso. Jesper, Carola, María, Inés, Gonzalo, Oscare, Abe, Juanpa y tantos otros erasmus compartimos toda clase de aventuras en la Thomas Morus, en Oude Markt, con las bicis y los viajes en tren. Mi hermanita belga, Flora, me cuidó como nadie, dank u txiki!

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Gran parte de la tesis la he realizado también en el Instituto de Recursos Naturales y Agrobiología (CSIC) de Sevilla. Sin la ayuda de Nacho, mi compañero de proyecto, esta tesis no hubiera sido la misma. Quillo, gracias por todo ese esfuerzo en el trabajo de campo, por enseñarme a desenvolverme en las parcelas experimentales, por los viajes en el Bellotín y por el trabajo en equipo que ha hecho posible esta tesis y los artículos que espero nos acepten pronto. Ha sido un placer también trabajar con Luís Ventura, quien me ayudó mucho con los análisis estadísticos multivariantes, y el resto de colegas del IRNA: Maite, Lorena, Cristina, Edu y Marisol, a la que siempre recordaremos como mucho cariño. Con Paco-laurel, compañero de la Universidad de Sevilla, compartimos muy buenos momentos en el campo, en el Picacho, y siempre nos echó una mano con cualquier duda estadística y con los datos climáticos.

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Itziar

Abril de 2008

Abstract

This Thesis addresses the study of the structure, dynamics and regeneration of *Q. suber* (cork oak)- *Q. canariensis* (Algerian oak) forests, located in Southern Spain (Los Alcornocales Natural Park, Cádiz-Málaga). The main objectives were: i) to identify the historical and environmental factors that have shaped forest composition and structure; and ii) to analyse differential regeneration patterns of both oak species along gradients of resource heterogeneity. The analyses were approached at several scales combining forest inventory data, cartographic information, filed work and modelling techniques.

As an introductory study we first analysed the distribution and regeneration of five *Quercus* and five *Pinus* species along climatic, edaphic and topographic gradients at regional scale (Andalusia), based on the Spanish Second Forest Inventory data (chapter 2). The following analyses were focused on the mixed *Q. suber- Q. canariensis* forests. First, we quantified forest composition changes during the 20th century from a series of historical forest inventories, and studied current forest structure along management and environmental gradients at various spatial scales (chapter 3). Second, seed sowing experiments were carried out along natural gradients of resource availability (light and water) in order to study inter-specific differences in the early stages of the regeneration cycle of *Q. suber* and *Q. canariensis*. Models of acorn survival to removal by animals (chapter 3) and models of seedling establishment (chapter 4) were parameterised as function of vegetation cover (light), soil water content, soil compaction and seed size.

Results showed that at regional scale *Quercus* species segregated along a gradient of water availability, whereas pines were associated with a gradient of temperature. Pine's regeneration was more abundant in forest areas without tree cover, while for *Quercus* species' regeneration occurred primarily under forest canopy. The distribution patterns found for *Q. ilex* and *Q. faginea* suggest that both oak species reach the coldest and driest areas thanks to the facilitation effect of pine canopy on oak seedling establishment.

Last-century forest management has shaped *Q. suber- Q. canariensis* forest structure and composition severely. A sharp increase in the density of *Q. suber* trees was found. This species was clearly favoured for cork production at the expense of *Q. canariensis*, particularly in more rainy areas, providing further evidence for humans as major drivers of oak forest composition across the Mediterranean. The impact of management is imprinted on the present-day forest structure; *Q. suber* dominates in most of the stands, whereas *Q. canariensis* is associated with moister habitats near streams. Given that *Q. canariensis* stands are currently protected as forest habitat, it would be reasonable to predict an upward trend locally, in those areas where forest management has modified forest composition.

Q. suber and *Q. canariensis* regeneration is scarce and seems to be limited by both biotic and abiotic factors. Once seeds reach the ground, a high proportion is removed by mice. The probability of seed removal increased with plant cover for the two oak species. Inter-specific differences in acorn removal were higher in open areas and disappeared in closed microhabitats, especially during a non-mast year. Despite later seed-drop, *Q. suber* acorns were removed at a higher proportion probably due to their larger seed size on average. In the next regeneration stages, autumn-winter heavy rains caused over-abundant soil water levels, associated with the more open habitats. Soil waterlogging reduced germination and emergence and lengthened time to emergence, which in turn decreased seedling survival during the dry season. Species mortality peaks occurred in different life stages.

There seems to be a conflict between demographic stages; microhabitats with a low removal risk for seeds (open) may exhibit less favourable conditions for subsequent seedling recruitment, and vice versa. Similarly, seed size effect in each stage was opposite; while smaller seeds showed higher probability to survive predation, seedlings from smaller seeds had overall decreased probabilities of germination and emergence.

Results suggest that between-year variation in precipitation could favour *Q. suber* and *Q. canariensis* species coexistence. We speculate that under not such rainy winters (without waterlogging) *Q. suber* would benefit, since it showed higher germination and emergence rates in humid but well drained soils. Conversely, *Q. suber* would be negatively affected by heavy rains due to its greater delay in emergence, which would result in a lower recruitment for this species. On the other hand, late spring rains and particularly sporadic summer rains seems to favour *Q. canariensis*. As a whole, the decrease of precipitations and increase of temperature predicted for the climate change process, will negatively affect both oak species regeneration.

Key words: emergence time, environmental gradients, heterogeneity, human impact, maximum likelihood, Mediterranean forest, seed size, seedling establishment, Strait of Gibraltar, survival.

Resumen

Esta Tesis Doctoral se centra en el estudio de la dinámica y estructura de los bosques de alcornoque (*Quercus suber*) y quejigo moruno (*Q. canariensis*) del Parque Natural Los Alcornocales (Cádiz, Málaga), con especial énfasis en los procesos de regeneración forestal. Los objetivos principales fueron: i) identificar qué factores históricos y ambientales han determinado la estructura actual de los bosques, y ii) analizar los patrones diferenciales de regeneración del alcornoque y el quejigo a lo largo de gradientes de heterogeneidad ambiental a pequeña escala. Se combinaron datos de inventarios forestales e información cartográfica, trabajo de campo y modelización.

En primer lugar, se abordó un estudió a escala regional para analizar la distribución de cinco especies de *Quercus* y de *Pinus* y su regeneración a lo largo de gradientes climáticos, edáficos y topográficos en Andalucía, a partir de los datos del 2º Inventario Forestal Nacional. Posteriormente, los análisis se centraron en los bosques mixtos de alcornoque y quejigo. Mediante el análisis de inventarios forestales históricos se estudiaron los cambios ocurridos en la composición de estos bosques a lo largo del siglo XX y se analizó la estructura actual de las masas mixtas a lo largo de gradientes ambientales y de manejo a varias escalas espaciales. En la segunda parte de la Tesis, se realizaron experimentos de campo y se construyeron modelos de la probabilidad de supervivencia del alcornoque y el quejigo en varias fases de su ciclo de regeneración, desde que las bellotas son dispersadas hasta el establecimiento de plántulas de un año. Se estudió el efecto de factores como el tamaño de la bellota, la compactación del suelo, el contenido de agua en el suelo y la cobertura vegetal (luz) en el éxito de transición entre las fases demográficas.

Los resultados de la Tesis muestran que a escala regional, las especies de *Quercus* aparecen principalmente asociadas a un gradiente hídrico y las especies de *Pinus* a un gradiente térmico. La regeneración de los pinos es más abundante en las zonas sin cobertura arbórea, mientras que los robles regeneran bajo el dosel arbóreo. Los patrones encontrados para *Q. ilex* y *Q. faginea* sugieren que su distribución alcanza las zonas más áridas y frías gracias al efecto del dosel de los pinares, que facilita el establecimiento de las plántulas de *Quercus*. En los bosques mixtos de alcornoque y quejigo la gestión forestal del último siglo ha determinado fuertemente su composición y estructura. En tan sólo un siglo la selvicultura ha favorecido al alcornoque para la producción de corcho, en detrimento del quejigo y otras especies, especialmente en las zonas con mayor régimen de precipitaciones. Actualmente, los quejigares están claramente asociados a los hábitats más húmedos cercanos a los cursos de agua, mientras que las masas de alcornocal dominan a medida que aumenta la distancia a los fondos de valle, incluso en las zonas con mayor coste de accesibilidad para la extracción de corcho. Dado que la presión sobre el quejigo ha cesado en las últimas décadas y que las actuales políticas de conservación y gestión forestal lo protegen, cabría esperar una tendencia a la recuperación de los quejigares localmente en aquellas zonas donde esta especie ha sido desplazada por la acción humana.

La regeneración natural de los bosques de alcornoque y quejigo es escasa y parece estar limitada tanto por factores bióticos como abióticos. Una vez que las bellotas caen al suelo por gravedad, experimentan unas tasas de remoción muy elevadas por la acción de los pequeños roedores, sobre todo en los años en que la producción de frutos es escasa. La probabilidad de remoción de bellotas se incrementó con la cobertura vegetal y las bellotas más grandes fueron seleccionadas preferentemente por los ratones. A pesar de la caída más tardía de las bellotas de alcornoque, éstas fueron removidas en mayor proporción que las de quejigo, posiblemente debido a su mayor tamaño promedio. Durante las fases demográficas siguientes, las fuertes lluvias de otoño-invierno causaron episodios de encharcamiento del suelo, asociados a los microhábitats con poca cobertura vegetal, que resultaron en una disminución de la probabilidad de germinación y emergencia de plántulas. Asimismo, el encharcamiento provocó un retraso en la emergencia de las plántulas, lo cual redujo su posterior probabilidad de supervivencia durante la sequía estival.

Se encontró un conflicto entre las fases demográficas estudiadas, donde los microhábitats con menor riesgo de depredación para las semillas (abiertos) fueron los menos favorables para el establecimiento de las plántulas. La influencia del tamaño de la bellota en cada fase fue opuesta; mientras las bellotas más pequeñas mostraron mayor probabilidad de sobrevivir a la acción de los depredadores, a su vez fueron las que menor probabilidad de germinación y emergencia presentaron.

Los resultados sugieren que la variabilidad interanual de las precipitaciones puede favorecer la coexistencia del alcornoque y el quejigo. Durante inviernos no muy lluviosos, sin encharcamiento, el alcornoque se beneficiaría respecto al quejigo por sus mayores tasas de germinación y emergencia bajo condiciones de suelo húmedo pero bien drenado. Sin embargo, ante lluvias intensas de otoño e invierno, el alcornoque experimentaría un mayor retraso en su emergencia que resultaría en un menor reclutamiento de esta especie. Por otra parte, las lluvias tardías de primavera y en especial las esporádicas de verano parecen favorecer al quejigo. De forma global, una reducción general en las precipitaciones y el aumento de la temperatura, como está previsto en el actual proceso de cambio climático, agudizará el problema de regeneración en estos bosques.

Palabras clave: bosque mediterráneo, establecimiento de plántulas, Estrecho de Gibraltar, gestión forestal, gradientes ambientales, heterogeneidad, máxima verosimilitud, supervivencia, tamaño de semilla, tiempo de emergencia.

Índice

Capítulo 1

Capítulo 1

Introducción general

Comprender los factores y mecanismos que regulan la estructura y dinámica de los ensamblajes biológicos es una cuestión fundamental de la ecología vegetal y de la biología de la conservación (Whittaker 1970; Crawley 1986; Huston 1994; Hubbell 2001). Los factores ambientales a gran escala, los factores locales, las perturbaciones, y las interacciones entre las especies determinan la dinámica y composición de las comunidades vegetales (Whittaker 1956; Grime 1979; Tilman 1990). Investigar de qué forma estos factores interactúan y controlan la distribución local de las especies de plantas ayuda a explicar la estructura y composición de las comunidades a lo largo de gradientes ambientales. Además, permite anticipar sus trayectorias futuras ante perturbaciones o cambios en las condiciones ambientales y por tanto, genera un conocimiento y una información esenciales para lograr una gestión de los ecosistemas más eficaz.

La creciente disponibilidad de observaciones sobre la distribución de especies, el acceso a información ambiental proveniente de muestreos sistemáticos, así como el desarrollo de métodos estadísticos con el creciente aumento de la capacidad computacional, han generado en las últimas décadas nuevas oportunidades para explorar la estructura de las comunidades vegetales a lo largo de gradientes ambientales (Franklin 1998; Guisan y Zimmermann 2000; Guisan y Thuiller 2005). El estudio de las comunidades vegetales se ha fundamentado en gran medida en el análisis de patrones espaciales estáticos y en la identificación mediante modelos correlacionales de los factores (climáticos, topográficos, edáficos) relacionados con los procesos fisiológicos más relevantes que inciden sobre la presencia o ausencia de las especies en un territorio (Goldberg 1982; Roberts y Wuest 1999; Cavender-Bares *et al.* 2004; Coudun *et al.* 2006). Sin embargo, son necesarios análisis de la estructura de las comunidades (abundancia de especies, estructura de edades o tamaños) que permitan evaluar su estado de conservación y ayuden a interpretar mejor la dinámica de las comunidades y predecir los cambios futuros, particularmente en áreas donde las especies encuentran factores limitantes (ambientales o perturbaciones) para su regeneración y por tanto para su persistencia.

La naturaleza de la escala espacial de observación y la dimensión temporal toman especial relevancia a la hora de estudiar la dinámica y estructura de las comunidades (Levin 1992; Urban 2005). Por un lado, existe una jerarquía de factores ambientales que operan a diferentes escalas espaciales en las relaciones vegetación-ambiente; la relevancia de los distintos procesos varía en función de la escala. De esta forma, a niveles superiores factores como el clima serán determinantes, mientras que a escalas espaciales menores los factores locales o las interacciones bióticas ejercerán un mayor control (Reed *et al.* 1993; Pearson y Dawson 2003). Por otro lado, los efectos históricos como los cambios en las condiciones ambientales, las perturbaciones o el impacto de las actividades humanas han determinado la estructura actual de las comunidades (McGlone 1996). Dado que los ecosistemas son sistemas dinámicos que varían en el tiempo según las fluctuaciones ambientales y los mecanismos de respuesta de sus componentes (Levin 1981), incluir la componente temporal o histórica puede ampliar la visión de la dinámica de las comunidades más allá de la que reconocemos en el paisaje actual (Foster *et al.* 2002).

Los modelos correlacionales (también conocidos como modelos "top down", sensu Landsberg 1986) describen de forma empírica la relación entre diferentes variables y sirven para inferir los posibles mecanismos subyacentes. Las relaciones vegetación-ambiente son resultado de interac-

ciones complejas y normalmente no lineales entre los factores abióticos y los rasgos ecofisiológicos específicos de cada especie, de las interacciones de competencia y facilitación dentro y entre especies, así como de procesos a nivel poblacional como la limitación en el reclutamiento. Además, todos estos procesos operan dentro de paisajes heterogéneos sujetos a perturbaciones naturales o de origen antrópico.

Por tanto, para profundizar en el conocimiento sobre la estructura y la dinámica de los ecosistemas es necesario conectar explícitamente la dinámica de poblaciones con los condicionantes ambientales mediante métodos cuantitativos; para ello se requiere tanto información descriptiva a nivel de comunidad como información experimental a nivel de individuo / población (ej., Pacala y Hurtt 1993; Purves *et al.* 2007). La combinación de técnicas empíricas y teóricas utilizadas recientemente en ecología forestal han supuesto un gran avance en la comprensión de los principales mecanismos que controlan los patrones de distribución y estructura de las comunidades. En las últimas décadas se han desarrollado modelos de proceso (o "bottom up", sensu Landsberg 1986) que intentan explicar o predecir la estructura y dinámica del bosque a partir de procesos que tienen lugar a niveles de organización inferiores, como por ejemplo procesos fisiológicos o procesos demográficos tales como la dispersión de semillas o la competencia (Shugart 1984; Pacala *et al.* 1996). Una vez que los patrones son detectados, y definidos como una descripción de la variación de la distribución de los organismos, el siguiente paso ha de identificar los factores determinantes de dichos patrones y los mecanismos que los generan y mantienen (Levin 1992).

Esta Tesis Doctoral se centra en el estudio de la estructura y dinámica de los bosques mediterráneos con especial énfasis en los procesos de regeneración forestal. Los bosques mediterráneos configuran paisajes muy heterogéneos, con una alta diversidad biológica, en los que las alteraciones debidas a las actividades humanas han jugado un papel determinante (Thirgood 1981; Blondel y Aronson 1995; Marañón y Ojeda 1998). Factores como la deforestación, la frecuencia de incendios y los cambios en los usos del suelo entre otros, han configurado en gran parte el paisaje mediterráneo actual (Blondel y Aronson 1999; Carrión *et al.* 2003). Por tanto, la acción antrópica durante los últimos milenios parece haber sido un elemento crítico de perturbación.

El estudio de los factores que controlan la distribución y composición de la vegetación mediterránea se ve limitado por la existencia de una estructura marcadamente antrópica que dificulta la aplicación de métodos convencionales de análisis de gradientes. Por otra parte, existe una información todavía limitada sobre la autoecología de las principales especies mediterráneas. En muchos casos no se conoce en profundidad qué factores han configurado la estructura y composición actual de los bosques, ni cómo las especies responden al estrés ambiental. Esta información es relevante a la hora de planificar una gestión forestal sostenible, más si cabe teniendo en cuenta los rápidos cambios que los ecosistemas forestales, particularmente en la región Mediterránea, están experimentando actualmente en su estructura causados por la fragmentación, los incendios o el abandono agrícola (OSE 2006). Además, estos ecosistemas aparecen como muy vulnerables al cambio en las condiciones ambientales que se prevén bajo los escenarios de cambio global (relativos a nuevos usos del suelo y a la variación en la temperatura y el régimen de precipitaciones), especialmente críticos para el sur de la cuenca Mediterránea (Schröter *et al.* 2005; IPCC 2007). Es necesario por tanto obtener un conocimiento básico de los procesos que controlan el establecimiento y desarrollo de las especies forestales, sus interrelaciones, así como su respuesta ante el estrés ambiental.

Estudios recientes en ecosistemas mediterráneos han demostrado la importancia de factores tanto abióticos como bióticos, así como la influencia de las perturbaciones en la composición de los bosques (Espelta *et al.* 1995; Pulido *et al.* 2001; Zamora *et al.* 2001). Concretamente los estudios empíricos muestran que la transición entre la fase de semilla y la fase de plántula es crítica, y puede ser clave para comprender la dinámica de los bosques mediterráneos (ej., Herrera *et al.* 1994; Jordano y Herrera 1995). La regeneración natural de la mayoría de las especies leñosas mediterráneas es escasa. En particular, es importante mejorar nuestro conocimiento de los requerimientos de la regeneración en las especies coexistentes de los bosques Mediterráneos. La luz y el agua parecen ser los principales factores que limitan el establecimiento de plántulas en ambientes mediterráneos, especialmente debido a la gran mortalidad de plántulas durante el periodo de sequía estival (Rey Benayas 1998; Marañón *et al.* 2004). La heterogeneidad de las condiciones del sotobosque afecta de forma diversa a la emergencia, la supervivencia y el crecimiento de las plántulas de las diferentes especies. Estas diferencias en el nicho de regeneración pueden contribuir a la coexistencia de las especies (Grubb 1977; Silvertown 2004). Dada la heterogeneidad tanto espacial como temporal de los recursos luz y agua en estos ecosistemas (Gómez-Aparicio *et al.* 2005; Quilchano *et al.* 2008), la respuesta diferencial de las especies bajo diferentes condiciones (sombra y disponibilidad de agua) en sus primeras etapas de desarrollo, determinan en gran medida la dinámica y composición del rodal a lo largo de gradientes ambientales (Zavala y Zea 2004). La aplicación simultánea de modelización y experimentación permite la formulación de modelos calibrados con datos de campo que retengan los aspectos esenciales de la biología del sistema e identifiquen aspectos que son críticos para el mantenimiento de la estructura de la comunidad (Pacala *et al.* 1996). El estudio de estos mecanismos y el uso de modelos son esenciales para escalar los procesos que operan a nivel de individuo a una escala de organización mayor y poder comprender la estructura de las comunidades en el paisaje.

Objetivo general de la Tesis Doctoral

La Tesis Doctoral tiene como objetivo principal estudiar los factores y procesos que controlan la dinámica y la composición del rodal en un bosque mediterráneo, en concreto en las masas mixtas de alcornoque (*Quercus suber* L.) y quejigo moruno (*Quercus canariensis* Willd.) de las sierras al norte del estrecho de Gibraltar (Parque Natural los Alcornocales, Cádiz-Málaga). Específicamente la investigación identifica qué factores históricos y ambientales han determinado la estructura actual de los bosques de alcornoque y quejigo, y analiza los patrones diferenciales de regeneración de las dos especies a lo largo de gradientes de heterogeneidad ambiental a pequeña escala que pueden ser determinantes para explicar la estructura del rodal y dinámica de estos bosques.

Para lograr este objetivo se han combinado análisis de gradientes a varias escalas espaciales y temporales, con datos experimentales y modelización. Así, en la primera parte de la investigación, y como introducción a los bosques de la zona de estudio, se analizaron los patrones de abundancia y el estado de regeneración de las principales especies forestales de Andalucía (géneros *Quercus* y *Pinus*) a lo largo de gradientes climáticos, fisiográficos y edáficos. Posteriormente, la investigación se centró en las dos especies de estudio, el alcornoque y el quejigo, incluyendo un análisis temporal de los cambios en su composición durante el último siglo y desarrollando estimadores estadísticos a partir de datos de inventarios forestales para identificar los principales factores abióticos y antrópicos que han determinado la estructura y composición actual de estos bosques a varias escalas espaciales. En la segunda parte de la tesis, se estudió la respuesta individual del alcornoque y del quejigo a las condiciones ambientales en el rodal (disponibilidad de luz y agua) parametrizadas con datos experimentales durante las fases principales del ciclo de rege-

neración, ya que los patrones diferenciales de reclutamiento de plántulas de las dos especies a lo largo de gradientes de heterogeneidad ambiental a pequeña escala pueden ser determinantes para explicar la estructura del rodal y predecir su dinámica. Por último, se ha elaborado una síntesis de los resultados obtenidos donde se discuten los procesos y factores que operan a diferentes escalas y determinan la estructura y regeneración de los bosques mediterráneos estudiados.

Estructura de la Tesis Doctoral y objetivos específicos de cada capítulo

La presente Tesis se ha organizado por capítulos en formato de artículos científicos. Tras este capítulo introductorio (capítulo 1), se presentan cuatro capítulos en inglés con sus correspondientes secciones de introducción, material y métodos, resultados y discusión, todos ellos precedidos de un resumen en castellano e inglés. Estos capítulos reproducen los contenidos de artículos en preparación (capítulo 2), en prensa (capítulo 3) y en revisión (capítulos 4 y 5) en diferentes revistas científicas. Por último, el capítulo 6 desarrolla la discusión general y el capítulo 7 presenta las conclusiones de esta Tesis Doctoral. Cada capítulo tiene su propia sección de referencias. A continuación se describe el contenido y los objetivos específicos de cada capítulo. La metodología concreta empleada en cada estudio se desarrolla con mayor detalle en los capítulos correspondientes.

Capítulo 2. *Desacoplamiento entre la distribución de los bosques de Pinus y Quercus mediterráneos y su regeneración a lo largo de gradientes ambientales: ¿Qué papel juega la facilitación?*

En el capítulo 2 se presenta un estudio sobre los patrones de distribución de los bosques mediterráneos y de su estado de regeneración a lo largo de gradientes ambientales en Andalucía, a modo de descripción global e introducción al objeto de la investigación. Se seleccionaron las diez especies arbóreas principales de esta región mediterránea: cinco especies del género *Quercus* [*Quercus ilex* (encina), *Q. suber* (alcornoque), *Q. faginea*, (quejigo), *Q. canariensis* (quejigo moruno), y *Q. pyrenaica* (roble melojo)], y cinco especies del género *Pinus* [*Pinus halepensis* (pino carrasco), *P. pinaster* (pino resinero), *P. pinea* (pino piñonero), *P. nigra* (pino laricio), y *P. sylvestris* (pino silvestre)]. Se analizó la estructura del rodal a partir de los datos del Segundo Inventario Forestal Nacional -IFN2- (MMA 1996). Cada parcela del inventario se caracterizó con información ambiental independiente (climática, edáfica, topográfica y de frecuencia de incendios) en un Sistema de Información Geográfica (SIG), con el objetivo de conocer el estado de regeneración de estos bosques y describir los patrones de segregación y coexistencia de las especies a lo largo de gradientes ambientales. Se dio especial énfasis al análisis comparativo entre la abundancia de adultos y de la regeneración (plántulas y juveniles) de cada especie, para comprobar si mostraban diferentes requerimientos ambientales, y se exploraron posibles interacciones (competencia, facilitación) entre los *Pinus* y *Quercus* a lo largo de los gradientes ambientales principales.

Las preguntas específicas que se formularon en este estudio fueron:

¿Cuáles son los factores principales (climáticos, topográficos, edáficos, frecuencia de incendios) que explican las diferencias en los patrones de abundancia de las especies de *Pinus* y *Quercus* en Andalucía?

¿Cuál es el estado de regeneración que presentan estos bosques?- en concreto ¿qué especies presentan un problema (falta o limitación) de regeneración?

¿Difiere el nicho de regeneración de las especies de la distribución de los adultos a lo largo de los gradientes ambientales principales?

Capítulo 3. *Factores ambientales y antrópicos como determinantes de la composición de los bosques del sur de la Península Ibérica: hacia un predominio del alcornoque debido al manejo forestal del siglo XX*

El capítulo 3 se centra en las dos especies principales de estudio, el alcornoque y el quejigo moruno, para analizar en detalle qué factores han determinado la estructura actual de estos bosques a lo largo de gradientes ambientales y de manejo. De esta forma, se llevó a cabo un análisis de la estructura actual de los bosques de alcornoque y quejigo a lo largo de gradientes ambientales a dos escalas espaciales, regional y de paisaje, incorporando respectivamente información climática e información topográfica derivada de un modelo digital del terreno (MDT). El diseño de muestreo del IFN2 con 1 km de resolución es el más completo y con mejor resolución espacial disponible a escala regional. Sin embargo, este tipo muestreo favorece a las especies abundantes, mientras que las especies más escasas o localizadas, como el quejigo moruno, quedan probablemente submuestreadas. De ahí la importancia de incluir información adicional de inventarios forestales con una resolución espacial menor (150 m) a escala de paisaje, proporcionada por las ordenaciones de montes.

Asimismo, se incorporó la escala temporal o histórica para conocer los cambios ocurridos en la composición de los bosques mixtos a lo largo del siglo pasado y evaluar la influencia que las actividades humanas más recientes (como la selvicultura) han podido ejercer sobre la composición de los bosques, aspectos que pocas veces se incluyen en este tipo de estudios biogeográficos. El factor antrópico es importante en el caso de especies como el alcornoque, cuyo aprovechamiento forestal principal (la producción de corcho para tapones) comenzó a finales del siglo XIX. Es por tanto probable que la componente económica haya determinado en gran medida la estructura de los bosques mixtos que observamos en la actualidad. Se analizaron las ordenaciones de montes e inventarios forestales llevados a cabo desde principios del siglo XX en nueve montes públicos del área del Parque Natural Los Alcornocales. Los cambios históricos en la composición de los bosques se relacionaron con las prácticas selvícolas, con indicadores socio-económicos como el precio del corcho y con las variaciones en la temperatura y precipitación ocurridas durante el último siglo en el área de estudio.

Las cuestiones concretas que se formularon fueron:

¿Cuál es la estructura actual de los bosques mixtos de alcornoque y quejigo a lo largo de gradientes climáticos y a lo largo de gradientes topográficos y de manejo?

¿Cómo han influido las actividades humanas en la estructura y composición de los bosques mixtos? - en concreto, ¿ha favorecido la selvicultura al alcornoque en detrimento de otras especies como el quejigo?

¿Han ocurrido cambios significativos en las condiciones ambientales (precipitación y temperatura) que hayan podido influir en la dinámica de los bosques durante el último siglo?

La segunda parte de la tesis doctoral, **Capítulo 4** y **Capítulo 5**, aborda el estudio de varias fases concatenadas del ciclo de regeneración del alcornoque y el quejigo: la remoción de bellotas que pueden ser depredadas o dispersadas por los animales consumidores (capítulo 4) y las fases de germinación, emergencia y supervivencia de plántulas (capítulo 5). Las diferencias que aparecen entre las especies durante estas fases tempranas juegan un papel decisivo en los patrones de

reclutamiento de nuevos individuos, que posteriormente pueden influir en la dinámica del bosque y determinar la segregación de las especies en el paisaje, especialmente en ambientes heterogéneos como los bosques mediterráneos. Las hipótesis de esta aproximación se basan en que tratándose de una especie esclerófila (el alcornoque) y otra semi-caducifolia (el quejigo), y dadas sus diferencias en la fenología y en el tamaño de semilla, ambas tendrán diferentes requerimientos de luz y agua y por tanto diferirán en sus nichos de regeneración. Para ello, se han parametrizado modelos de la probabilidad de supervivencia de los individuos para cada fase estudiada ajustando diferentes formas funcionales que cubren un amplio rango de posibles respuestas de las especies a los gradientes explorados. Esta aproximación permite identificar los ejes estratégicos a lo largo de los cuales las especies se diferencian (Kobe 1999).

Estos dos capítulos tratan de identificar los factores principales que limitan el reclutamiento de plántulas de las dos especies y de parametrizar la respuesta individual de cada especie a la heterogeneidad ambiental en sus primeras etapas de desarrollo para responder a las siguientes cuestiones:

¿Difieren el alcornoque y quejigo en su respuesta a los gradientes espaciales y temporales de disponibilidad de recursos (luz y agua) a pequeña escala en las fases estudiadas de su ciclo de regeneración?

¿Qué implicaciones ecológicas tienen los procesos de regeneración en la dinámica forestal y en la coexistencia de las especies de estudio?

Capítulo 4. *Remoción de bellotas de Quercus suber y Q. canariensis: consecuencias ecológicas del tamaño de semilla, de la cobertura vegetal y de la temporalidad en la caída de la bellota*

En concreto, en el capítulo 4 se estudiaron las tasas de remoción de bellotas de alcornoque y de quejigo colocadas experimentalmente sobre un suelo forestal (durante tres meses) a largo de un gradiente amplio de cobertura vegetal en dos años consecutivos. Se simuló el proceso de dispersión abiótica más común (por gravedad). Desde que las bellotas caen del árbol hasta que germinan pueden ser removidas por animales, principalmente roedores o aves, pero también por coleópteros coprófagos como *Thorectes lusitanicus*, descrito para nuestro sistema de estudio por Pérez-Ramos (2007). Estos animales pueden actuar como depredadores limitando la regeneración de las especies, aunque también pueden jugar un papel importante como dispersores secundarios. Los objetivos de este estudio fueron analizar si existía preferencia por alguna de las dos especies de estudio y si esta fase suponía un cuello de botella que limita el reclutamiento de nuevos individuos. Se construyeron modelos de la probabilidad de remoción de bellotas para el alcornoque y el quejigo en función de la estructura del hábitat (captando un gradiente continuo de cobertura vegetal), incluyendo el efecto del tiempo de la caída de la bellota y el tamaño de la semilla.

Capítulo 5. *La heterogeneidad del agua en el suelo y el tiempo de emergencia controlan el establecimiento de plántulas de tres especies de Quercus*

La diferente respuesta de las especies arbóreas a la disponibilidad de recursos como la luz y el agua durante la fase crítica del establecimiento de plántulas puede influir en la dinámica forestal. Los estudios en bosques mediterráneos se han centrado fundamentalmente en el análisis de los efectos de la sombra y de la sequía estival en la supervivencia de plántulas. Sin embargo, no se conocen los efectos de las lluvias que caen desde el otoño hasta la primavera sobre las etapas

más tempranas (germinación y emergencia) del ciclo de regeneración. En el capítulo 5 se presentan los resultados de un experimento de siembra de bellotas de alcornoque y quejigo a lo largo de gradientes naturales y continuos de disponibilidad de luz y agua (durante los periodos húmedo y seco). Se incluyó también el roble melojo (*Quercus pyrenaica*), que forma pequeños rodales en las zonas de cumbre en el área de estudio, si bien para esta Tesis Doctoral son más relevantes los resultados descritos para el alcornoque y el quejigo. Las etapas de germinación de bellotas, emergencia de plántulas y supervivencia se monitorizaron durante un año y se construyeron modelos para cada fase y especie en función de la luz, el contenido del agua en el suelo y la compactación del suelo. Se estudió el efecto del riego, simulando lluvias esporádicas, sobre la supervivencia de las plántulas durante el periodo estival. Asimismo, se estudió la influencia de factores como el tiempo de emergencia y la variación del tamaño de bellota en el éxito de la regeneración natural de las especies de estudio, que pueden jugar un papel determinante en la dinámica de la regeneración de los bosques mediterráneos de *Quercus*.

Capítulo 6. *Discusión general: síntesis a multiescala*

En el capítulo 6 se presenta una síntesis de los resultados de los cuatro capítulos anteriores tratando de integrar cómo los factores ambientales analizados explican la distribución y regeneración de las especies a distintas escalas espaciales (regional, de paisaje, de rodal y de micrositio) abordadas a lo largo de la tesis. Asimismo, se discute si la respuesta diferencial del alcornoque y el quejigo a la heterogeneidad ambiental a pequeña escala (gradientes de luz y agua) en las primeras fases de su ciclo de regeneración son clave para explicar la estructura de las masas mixtas y para predecir la dinámica de la regeneración de estos bosques.

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Capítulo 2

Capítulo 2

Desacoplamiento entre la distribución de los bosques de *Pinus* y *Quercus* mediterráneos y su regeneración a lo largo de gradientes ambientales: ¿Qué papel juega la facilitación?

Este capítulo reproduce el texto del siguiente manuscrito:

Urbieta, I.R., García, L.V., Zavala, M.A. and Marañón, T. Uncoupling of Mediterranean pine-oak forest distribution and regeneration along environmental gradients: does facilitation matter? (*In preparation*).

Resumen

Los factores ambientales, las perturbaciones y las interacciones entre especies determinan ensamblajes biológicos a diferentes escalas espaciales. Un mejor conocimiento de la estructura de los bosques y de los procesos de facilitación de las especies a lo largo de gradientes ambientales puede ayudar a anticipar la respuesta de las comunidades vegetales ante cambios ambientales y es de utilidad para el desarrollo de programas de restauración forestal. El objetivo de este estudio es describir de forma cuantitativa las relaciones vegetación-ambiente en cinco especies de pinos (*Pinus halepensis*, *P. pinaster*, *P. pinea*, *P. nigra*, *P. sylvestris*) y cinco especies de *Quercus* (*Q. ilex*, *Q. suber*, *Q. faginea*, *Q. canariensis*, *Q. pyrenaica*) del sur de la Península Ibérica, poniendo especial énfasis en el análisis de la distribución de los adultos y de la regeneración forestal (plántulas y juveniles) para comprobar si muestran diferentes requerimientos ambientales. Se caracterizaron 12.572 parcelas del segundo Inventario Forestal Nacional con información climática, edáfica, topográfica y de la frecuencia de incendios en un sistema de información geográfica. Se analizaron las diferencias en abundancia (área basal) entre adultos y regenerado a lo largo de los gradientes ambientales principales mediante un análisis canónico de correspondencias (CCA) y modelos lineales generalizados (GLZs). El gradiente térmico determinó la segregación de las especies de pinos, mientras que la precipitación de invierno explicó la distinta distribución de los *Quercus*, siendo el contenido de calcio en el suelo un factor determinante en la distribución de algunas especies. Aproximadamente un 45% de los rodales de pino mostraron una limitada regeneración, mientras que en los *Quercus* este porcentaje varió entre un 20% y un 60%, alcanzando los valores más altos en el alcornoque (*Q. suber*) y en el quejigo moruno (*Q. canariensis*). La regeneración de los pinos se encontró fundamentalmente bajo el propio dosel de los pinares y de forma importante en zonas abiertas sin cobertura arbórea, reflejando su capacidad colonizadora. En cambio, en algunos *Quercus* las condiciones ambientales en las que se encontraron los adultos y el regenerado divergieron. En el caso de la encina (*Q. ilex*) y el quejigo (*Q. faginea*), la abundancia de regeneración fue mayor bajo el dosel de los pinares, particularmente en las zonas con mayor limitación ambiental, es decir, en las zonas más frías y áridas, donde no se encontraban encinares ni quejigares, lo que sugiere que los pinares pueden estar ejerciendo un efecto de facilitación en el establecimiento de estas especies de *Quercus*, con el resultado de una expansión de sus nichos realizados. Los resultados de este estudio ponen de manifiesto la importancia de las interacciones entre los pinos y los *Quercus* en la estructura de los bosques mediterráneos, e identifican un problema global de falta de regeneración en los bosques que debe abordarse en los planes de conservación y restauración.

Uncoupling of Mediterranean pine-oak forest distribution and regeneration along environmental gradients: does facilitation matter?

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Abstract

Environmental drivers, disturbance processes, and species interactions determine biological assemblages at different spatial scales. Improved understanding of forest structure and facilitation processes along environmental gradients gives insights for the development of tools for ecosystem restoration, and for anticipating the response of plant species and communities to key environmental change drivers. The aim of this study was to quantitatively describe vegetation-environmental relationships of five pine species (*Pinus halepensis*, *P. pinaster*, *P. pinea*, *P. nigra*, *P. sylvestris*) and five oak species (*Quercus ilex*, *Q. suber*, *Q. faginea*, *Q. canariensis*, *Q. pyrenaica*) in southern Iberian Peninsula, with emphasis on the differences between adults' environmental requirements and those of seedlings and saplings (regeneration). 12572 forest inventory plots were characterized with climatic, edaphic, topographic and fire frequency data in a geographical information system. Differences in adult and regeneration abundance (basal area) along the main environmental gradients were analysed by canonical correspondence analysis (CCA) and generalized linear models (GLZs). Pine species segregated along a gradient of temperature, whereas oaks were associated with the winter precipitation gradient; with soil calcium content as a key factor for some species. Around 45% of pine forest stands showed a limited regeneration, whereas in oak stands this percentage varied from 20% up to 60% in some species, with highest proportion for *Q. suber* and *Q. canariensis*. Pines' regeneration occurred mainly under the canopy of pine forests, and significantly in areas without tree cover, reflecting their colonizer ability. Conversely, some oak species diverge substantially in the environmental conditions under which canopy trees and recruits were found. Oak regeneration was highest in pine-dominated stands (for *Q. ilex* and *Q. faginea*), particularly in areas with increasing environmental severity, i.e., in the coldest and more arid extremes of the environmental gradients explored; this suggests that a possible facilitative effect of pine forests on the establishment of oak species might be occurring, which provides an expansion of oaks' realized niches. Results show the importance of pine-oak interactions in driving Mediterranean forest structure, and identify a regeneration problem in most of the studied species that would need urgent action through conservation and restoration programmes.

Keywords: Gradient analysis; niche-based model; pines; oaks; Mediterranean forest; facilitation; forest regeneration.

Introduction

A fundamental issue to conservation biogeography is to interpret the manner in which broad environmental drivers, local sites factors and disturbance processes interact to control patterns and changes in biological assemblages at different spatial scales (Grime 1979; Huston 1994). Our ability to understand current ecosystem structure, composition and function is key to address conservation management and restoration ecology more effectively.

Ecosystems are dynamic as a consequence of disturbance and environmental change which interact with biological processes, including species ability to reproduce and disperse (i.e., colonization of adjacent habitats) and species positive and negative interactions (i.e., competition and facilitation). Main broad-scale vegetation controls appear to be climatic and historical constraints, such as geographical dispersal limitation, which have strongly conditioned current species distribution ranges (Montoya *et al.* 2007; Svenning and Skov 2007). At a more local scale, soil factors can determine plant species distribution in the landscape (Roberts and Wuest 1999; Coudun *et al.* 2006). Furthermore, there is a clear linkage between ecosystem history and current pattern and processes that makes increasingly necessary that long-term perspectives are integrated into plant species distribution studies (Foster *et al.* 2002).

Since distribution and abundance of many plant species are influenced by the presence of others, inter-specific interactions can be very important in determining species coexistence (Pacala *et al.* 1996; Callaway and Walker 1997). Community composition is regulated by plant-plant interactions, which can change along environmental gradients from facilitation to competition (Holmgren *et al.* 1997; Pugnaire and Luque 2001; Sthultz *et al.* 2007). Net positive interactions (i.e., the beneficial impacts of neighbours) are likely to occur with increasing environmental severity as reported in recent studies (e.g., Maestre *et al.* 2003; Gómez-Aparicio *et al.* 2004). Bruno *et al.* (2003) discussed a revision of the niche theory to include the potential for expansion of the realized niche of species by facilitation (as empirically demonstrated by Hacker and Gaines 1997; Choler *et al.* 2001). Thus, because positive interactions alleviate abiotic stress, the distribution of a species (realized niche) could be expanded by facilitative interaction with its neighbours. Studies looking at species interactions often examine one particular species pairing, but few have attempted to take a broader approach and examine patterns at the community level and across gradients.

Plant resources (i.e., light availability, nutrient supply, or water regime) can change significantly through the life of individuals. Tree seedlings have smaller and shallower root systems than mature trees, and occur in soil layers most susceptible to drying from soil surface evaporation and transpiration of neighbouring trees and herbaceous layer (Weltzin and McPherson 1997; Kolb and Stone 2000). Thus, there might be changes in carbon and water relations (e.g., drought response strategies and differences in photosynthetic capacity) with ontogeny, i.e., between seedlings, saplings and mature trees (Cavender-Bares and Bazzaz 2000; Mediavilla and Escudero 2004; Quero *et al.* 2007). Consequently, effective regeneration might be distant (under different resource conditions) from adults, associated with certain microhabitats within a forest or located in areas where the tree layer is absent.

Although, plant species' environmental limiters provide clues to reconstruct species past distribution and restore ecosystems (Arundel 2005), it is crucial to assess how populations, e.g. forest stand structure, vary along environmental gradients. Specially important in areas where natural regeneration is scarce or where species find constraints (environmental or disturbances)

for regeneration, and thus, persistence. Most tree species biogeography studies however, often focus on species presence/absence data, and overlook population structure behind and species interactions along environmental gradients.

This study analyses the relationship between the abundance of five oak (*Quercus* spp.) and five pine (*Pinus* spp.) species and several environmental factors (climatic, topographic, soil characteristics, and fire frequency) in Andalusia region (Southern Spain), based on forest inventory data linked to independent environmental information in a Geographical Information System (GIS). The aim was to study the relative contribution of the complex abiotic environment to explain species distribution and forest structure, in order to characterise species' environmental niches (i.e., realized niches), and to explore whether environmental requirements of adult canopy trees differed from those of saplings and seedlings (i.e., advance regeneration).

Pine and oak forests are major structural components of Mediterranean ecosystems (see Richardson 1998; Quézel 2000; Rouget *et al.* 2001; Purves *et al.* 2007). Both natural and anthropogenic disturbances (i.e., wildfires, forest management etc.) have governed pine and oaks dynamics at various spatio-temporal scales (Zavala *et al.* 2000; Carrión *et al.* 2003; Benito Garzón *et al.* 2007). In recent times, particularly over the twentieth century, forest management has traditionally encouraged land cover changes in Mediterranean landscapes. For example, forest restoration techniques relied on the establishment of tree cover for soil conservation purposes, mainly by means of extensive plantations of fast growing pioneer species such as pines, in natural or degraded ecosystems, assuming this species would facilitate the establishment (artificial or natural) of late-successional species such as oaks (Gil and Prada 1993; Pausas *et al.* 2004b). The fingerprint of such widespread management may still be reflected in present-day forest structure. With this purpose, we analysed pine and oak forest regeneration and stand structure along environmental gradients, with emphasis on identifying those species with a limited regeneration, and evaluating if oaks regenerated under the canopy of pine forests. Specifically we address the following questions: (1) What are the main factors (climatic, topographic, edaphic, fire frequency) determining intra- and inter-genera differences between pine and oak species abundance distribution? (2) What is the proportion of stands with limited regeneration for oak and pine species ? (3) What are the types of habitat in which pine and oak regeneration is present? (3) Does species regeneration niche differ from adult's environmental niche with respect to critical environmental factors? (4) Is oak regeneration effective under the canopy of pine forests?

Material and methods

Study region and species

The study area is located in Andalusia (southern Iberian Peninsula), region of ~ 87600 km^2 which encompasses a large altitudinal gradient (0-3480 m) (Fig. 2.1). Mountain systems surround the region and lie to both sides of the Guadalquivir Depression, with palezoic materials and siliceous rocks to the north (i.e., Sierra Morena) and sendimentary materials (limestone) originated in the Alpine orogeny to the south (i.e., Betic mountain ranges); main soil types found in the region are summarized in Appendix 2.1. The climate is Mediterranean but quite variable, with mean annual precipitation ranging from 140 mm up to 1400 mm. Dry and warm summers (average July temperature: 15 ºC to 27 ºC) are followed by fairly cold winters (average January temperature: -2 ºC to 12 ºC). The landscape is a mosaic of semi-natural forests, dehesas (oak savannas), shrublands, grasslands, intensive agricultural fields, and urban areas. Forest areas are absent in the most arid south-eastern territory, and have been almost eliminated by agricultural transformation from the River Guadalquivir valley (Fig. 2.1).

For the purpose of this study, we focused on five oak (*Quercus*) species and five pine (*Pinus*) species representative of Mediterranean forests: evergreens *Quercus ilex* and *Q. suber*, and winter deciduous *Q. faginea*, *Q. canariensis* and *Q. pyrenaica*; *Pinus* halepensis, *P. pinaster*, *P. pinea*, and montane *P. nigra* and *P. sylvestris* (see species distribution in Fig. 2.1). Selected species are major structural components of forests and woodlands covering the greatest part of the forest surface in Andalusia (in approximately 70% of the SSFI plots pine and/or oak presence was found). Forests harbour a rich biodiversity; and provide valuable socio-economic resources (cork, timber, acorns, pine cones, resins, etc.). Furthermore, most of these species are used in forest restoration programs. We analysed all SSFI plots including stands with native trees but that might had been planted in the past, due to the difficulty to disentangle their true origin. Exotic pine species (*P. radiata* and *P. canariensis*), present in less than 1% of plots, were excluded for the analyses.

Data set

Permanent plots of the Spanish Second Forest Inventory (SSFI) were chosen as sampling/mapping units. Wooded areas in Andalusia were inventoried between 1994 and 1996, with an intensity of approximately one circular plot per square kilometer (MMA 1996). The information (provided by province) was first processed separately and then gathered all (8 provinces) in one single database. Previous to the analyses, we checked the geographic position of all inventoried plots, superimposing them onto forest areas of recent digital orthophotographs (JA 2003). Plots with georeferencing errors were discarded for the analyses, giving a total of 12572 plots. Each forest inventory plot was characterized with independent environmental data according to their relevance to tree survival and growth, including climatic, topographic, soil characteristics, and fire frequency (see below for selected variables). We combined raster maps and sampling locations (UTM coordinates) for each species data to determine the values of each environmental variable in each SSFI plot using a GIS (ArcView 3.2, ESRI Inc., Redlands, USA, 2000).

Stand structure. - SSFI plots were circular of various concentric radii up to 25 metres, and were defined by their spatial location (UTM coordinates of the centre of the plot). Trunk diameter at breast height (dbh, 1.30 m) of all trees with a dbh greater than 7.4 cm was measured by two perpendicular measurements with a calliper. The minimum measured dbh varied with the radii of the plot: 7.5 cm dbh (5 m radius), 12.5 cm dbh (10 m), 22.5 cm dbh (15 m), 42.5 cm dbh or grater (25 m). For saplings (2.5-7.4 cm dbh) the number of individuals (density) was estimated within 5 m radius circle; we assumed a mean diameter of 5 cm per individual for basal area calculation. For seedlings (dbh < 2.5 cm) only their presence or absence was recorded within 5 m radius; if present, we assumed to be at least one seedling of 1.25 cm diameter in order to differentiate them from zero values (i.e., absences). Species basal area was calculated as the addition of the basal areas (m^2) of all trees of the same species present in each plot (assuming a circular cross-section of the trunk), and then expressed on a unit area basis, i.e., in square meters per hectare (m^2/ha). For the analyses, we first considered species abundance as the total basal area, i.e., the addition of all inventoried tree sizes. Then, we divided this value in two, as the sum of the basal areas of trees with a dbh > 7.4 cm, i.e., hereafter *adults* "a", and the basal areas of individuals with a diameter = 7.4 cm including saplings and seedlings, i.e., hereafter *regeneration* "r".

Climatic factors. - Climatic data with 1 km spatial resolution was provided by the Spanish Institute of Meteorology (INM) as an interpolation (kriging) of the information recorded from 1971 to 2000 in meteorological stations spread all over the Spanish territory (143 main stations, 1504 thermometric, and 4835 pluviometric stations) (INM unpublished). We assigned the

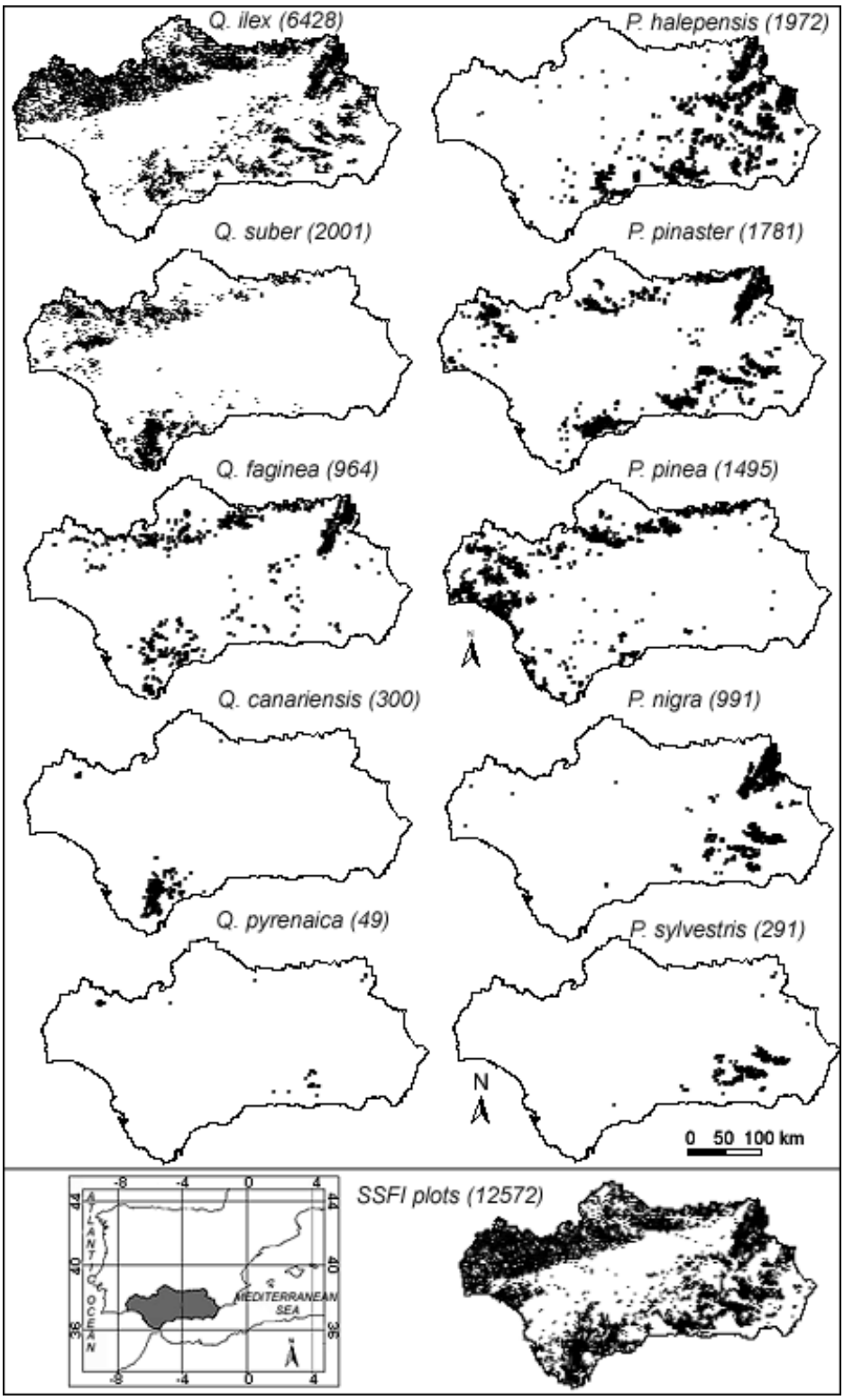

Figure 2.1 *Quercus* and *Pinus* species distribution in Andalusia (S Iberian Peninsula) based on SSFI plots (the number of plots per species is indicated in brackets).

following climatic variables to each SSFI plot: Monthly and annual mean precipitation (PANU) (mm), from which spring (PSPR), summer (PSUM), autumn (PAUT), and winter (PWIN) precipitation were calculated. Monthly and annual mean radiation (RADANU) (kwh/m^2), from which radiation per season was derived (RADSPR, RADSUM, RADAUT, RADWIN). Monthly and annual mean temperature (TANU) (ºC), from which the average temperature of the warmest month (TWM), average temperature of the coldest month (TCM), and thermal oscillation (TOSIC) were calculated. Monthly and annual potential evapotranspiration (TPET) (mm) were obtained as a function of mean temperature (Thornthwaite 1948). Computing monthly differences between P and PET we calculated annual water surplus (TSUP) as the sum of positive differences, annual water deficit (TDEF) as the sum of negative differences, and drought length (DL) as the number of months in which PET exceeded P.

Topographic factors. - Altitude (m) (ALT), slope (degrees) (SLOP), and aspect (degrees with respect to north) (ASP) of each SSFI plot were derived from a 20 m digital elevation model (DEM), obtained from colour aerial photograms (scale 1:60000, provided by REDIAM, the Environmental Information Network, Junta de Andalucía). Aspect directional data were subjected to inverse polar transformation, which produced two Cartesian variables accounting for slope orientation in the south-to-north (SN) and west-to-east (WE) directions.

Soil factors. - We assigned the dominant soil typological unit (named according to the FAO-UNESCO soil legend) to each SSFI plot, from the soil geographical database of Europe, escale 1/1000000, included in the European Soil Database v 1.0 (European Soil Bureau 1999) (Appendix 2.1). Using the FAO-UNESCO definition criteria for the different soil units, we derived ordinal categories for some relevant soil properties: soil depth (SDEPTH); soil base saturation (SBASE); presence of $CaCO_3$ (or in a few sites other calcium-rich materials as gypsum) in the soil (SCALC). We also used other attributes included in the soil database and derived estimates for overall soil water capacity (SAWC, mm), using the estimates for topsoil and subsoil water capacity given in European Soil Database (European Soil Bureau 1999).

Fire frequency. - Cartographic layers of fire surface, with a cover of at least 10 hectares, were elaborated based on Landsat images of Andalusia at the end of each fire campaign. Fire occurrence (FIRE) between 1987 and 2002 expressed in frequency was assigned to each SSFI plot. This information was provided by REDIAM (Junta de Andalucía unpublished).

Statistical analysis

Species abundance patterns

A Canonical Correspondence Analysis (CCA, ter Braak 1986) was carried out to study the relationship between species abundance and environmental variables (climatic, soil, topographic factors, and fire frequency). Basal area data were log transformed (log x+1) to minimize bias. To avoid artefacts, results were checked for uni- and multivariate extreme values (ter Braak and Smilauer 2002). Manual selection and Monte-Carlo permutation test ($p< 0.01$), with 999 unrestricted permutations under full model, were used for the selection of the most significant variables from the explanatory set, as well as to evaluate the significance of extracted axes. The stepwise option was used to exclude highly redundant environmental variables and to accurately detect the best predictors in the model (Økland and Eilertsen 1994; Vandvik and Birks 2002), excluding those with VIF (variance inflation factor) greater than 20. Environmental variables and tree species abundance were plotted in the environmental space (CCA biplots). CANOCO software v. 4.5 was used for these statistical analyses (ter Braak and Smilauer 2002).

To account for the spatial component, variance partitioning was performed by using the canoni-

cal modelling developed by Borcard *et al.* (1992), and Borcard and Legendre (1994). The overall species variance was partitioned into four components: (1) a non-spatially-structured component which is explained by the environmental variables, (2) a spatially-structured component explained by the environmental variation, (3) a spatially-structured component which is not explained by the environmental variables, possibly related to community dynamics, and (4) a residual, non-explained fraction. The relative importance of the three first components provides further insights into community organization (Maltez-Mouro *et al.* 2005, 2007). Significance was fixed at the 0.05 level throughout the study. Since repeated tests were carried out, corrections to limit type I error inflation were performed according to García (2004).

We analysed *Quercus* and *Pinus* species responses along the main CCA axes and the most relevant environmental variables, and fitted GLZs (Generalized Linear Models) (see Guisan *et al.* 2002), which were selected following the Akaike's Information Criteria (AIC, Akaike 1992) using the Canodraw for Windows program (ter Braak and Smilauer 2002). We tested for a bell-shaped unimodal response of species along the underlying environmental gradients, which is the form usually assumed to describe vegetation-environment relationship (ter Braak 1985; Whittaker 1978; Retuerto and Carballeira 2004; but see Austin 2002; Oksanen and Minchin 2002). Because of the skewed distribution of species' abundance, the huge quantity of absence data (i.e., species basal area equal to zero), and the positive response values, we assumed a Poisson distribution, log-link option, according to Leps and Smilauer (2003).

Adults versus regeneration

We analysed inter-specific differences in species' realized niches (all the inventoried individuals included, see above), and furthermore, we also compared the distribution patterns between adults and regeneration intraspecifically. First, adult/regeneration proportion found for each species in SSFI plots was analysed, with emphasis on describing the type of habitat (under canopy or in open-shrubby areas) in which species regenerate, and identifying species with a limited regeneration. Second, we compared 95% confidence intervals of adults and regeneration along CCA axes using the Canodraw for Windows program facilities. Finally, we analysed by means of GLZs if the abundance of canopy trees and recruits differed along the main environmental gradients.

Results

Species abundance along environmental gradients

The ranges of environmental conditions (for each of the initially selected abiotic factors, i.e., climatic, topographic and soil variables) for *Quercus* and *Pinus* species are summarized in the Appendix 2.2.

Distribution of oaks and pines was non-random and CCA results were highly significant. The global model (considering all extracted axes) explained nearly 23% of the overall species variance. The three main axes alone explained 18.4% of the overall species data, which means 86.6 % of the explained species variance (Table 2.1). The three first CCA axes were significant at $p< 0.001$ based on Monte Carlo 999 permutation tests. Axis 1 explained 9.5% of overall species variance, while Axis 2 a variance of 5.9 %, and Axis 3 accounted for 3%. In all cases, climatic variables entered first, followed by soil and topographic variables last, while fire frequency did not enter as a significant predictor. Those species with larger number of samples tend to have increased model success, except *Q. faginea* and *P. pinaster* which showed a low fitted variance. Species with more limited distribution such as *Q. pyrenaica* and *P. sylvestris* were difficult to analyse for the coarse scale data to capture, and thus had a low model success (Table 2.1).

CCA first two axes were interpreted by means of intra-set correlations and ordination biplots (Table 2.1, Fig. 2.2). Axis 1 was strongly and positively correlated with the temperature of the coldest (r= 0.9) and warmest (r= 0.7) months, and negatively with summer precipitation (r= -0.7) and radiation (r= -0.56). Altitude was not included in the model due to its strong negative correlation with temperature and positive correlation with summer precipitation, but indirectly defines Axis 1, increasing towards the negative extreme (r= -0.9). Edaphic and topographic factors such as soil calcium content (r= -0.6), soil depth (r= 0.56), soil base saturation (r= -0.45), and slope (r > -0.3), were also captured by Axis1. Axis 2 was strongly correlated with water availability conditions, positively with drought length (r= 0.65), and negatively with winter precipitation (r= -0.70). It also showed positive correlation with soil water storage capacity (r > 0.45), and temperature of the warmest month (r= > 0.5) (Table 2.1, Fig. 2.2).

Partial canonical correlation analysis (pCCA) showed that climatic variables had the highest unique contribution (53%) to the explained species variance, while topographic (slope) and soil related variables had a unique contribution of just 18%. The remained fraction (29%) of species' variance explained was a shared contribution of the two groups of factors. Therefore the climatic set alone accounted for 82% of the

Table 2.1 Explained variance for each of the first three CCA Axes, their correlation with the environmental variables, and fitted variance per species (see main text for abbreviations).

	CCA Axis 1	**CCA Axis 2**	**CCA Axis 3**
Eigenvalues :	0.58	0.35	0.18
Species-environment correlations :	0.82	0.65	0.48
Explained variance (% species data) :	9.50	5.90	3.00
Cumulative (%) of species data :	9.50	15.40	18.40
Cumulative (%) of species-envir. relation :	44.60	72.40	86.60
Weighted correlations			
SLOP	-0.32	-0.18	0.42
PSUM	-0.69	-0.33	-0.23
PWIN	0.54	-0.70	0.17
DL	0.22	0.67	0.27
RADSUM	-0.56	0.35	-0.56
TWM	0.70	0.52	-0.31
TCM	0.90	0.20	0.24
SBASE	-0.45	0.22	0.05
SCALC	-0.59	0.15	0.46
SDEPTH	0.56	0.32	0.00
SAWC	0.20	0.46	-0.19
Fitted variance (%)			
Q. ilex	0.97	4.00	20.20
Q. suber	29.82	41.12	44.81
Q. faginea	0.48	1.11	1.18
Q. canariensis	3.04	6.16	6.96
Q. pyrenaica	0.01	0.02	0.02
P. halepensis	11.88	23.09	32.58
P. pinaster	2.79	4.12	4.12
P.pinea	7.39	15.13	15.16
P.nigra	25.89	39.15	39.22
P.sylvestris	2.24	3.74	3.95

explained species variance, while topographic and soil-related variables alone were able to account for 47% of the explained species variance. Table 2.2 summarises the sequential analyses carried out for variance partitioning calculation, including: (1) unconstrained (CA); (2) stepwise CCA selecting the best, non-redundant, environmental predictors; (3) stepwise CCA selecting the best, non-redundant, spatial predictors; (4) stepwise partial CCA after adjusting by the best spatial set obtained in step 3; and (5) stepwise partial CCA using only spatial predictors, after adjusting for the best environmental set obtained in step 2. According to results, nearly 23% of species variance may be explained using spatial and environmental predictors. However, most of the explained species variance (72%) was spatially structured, while only a 28% was independent of the space.

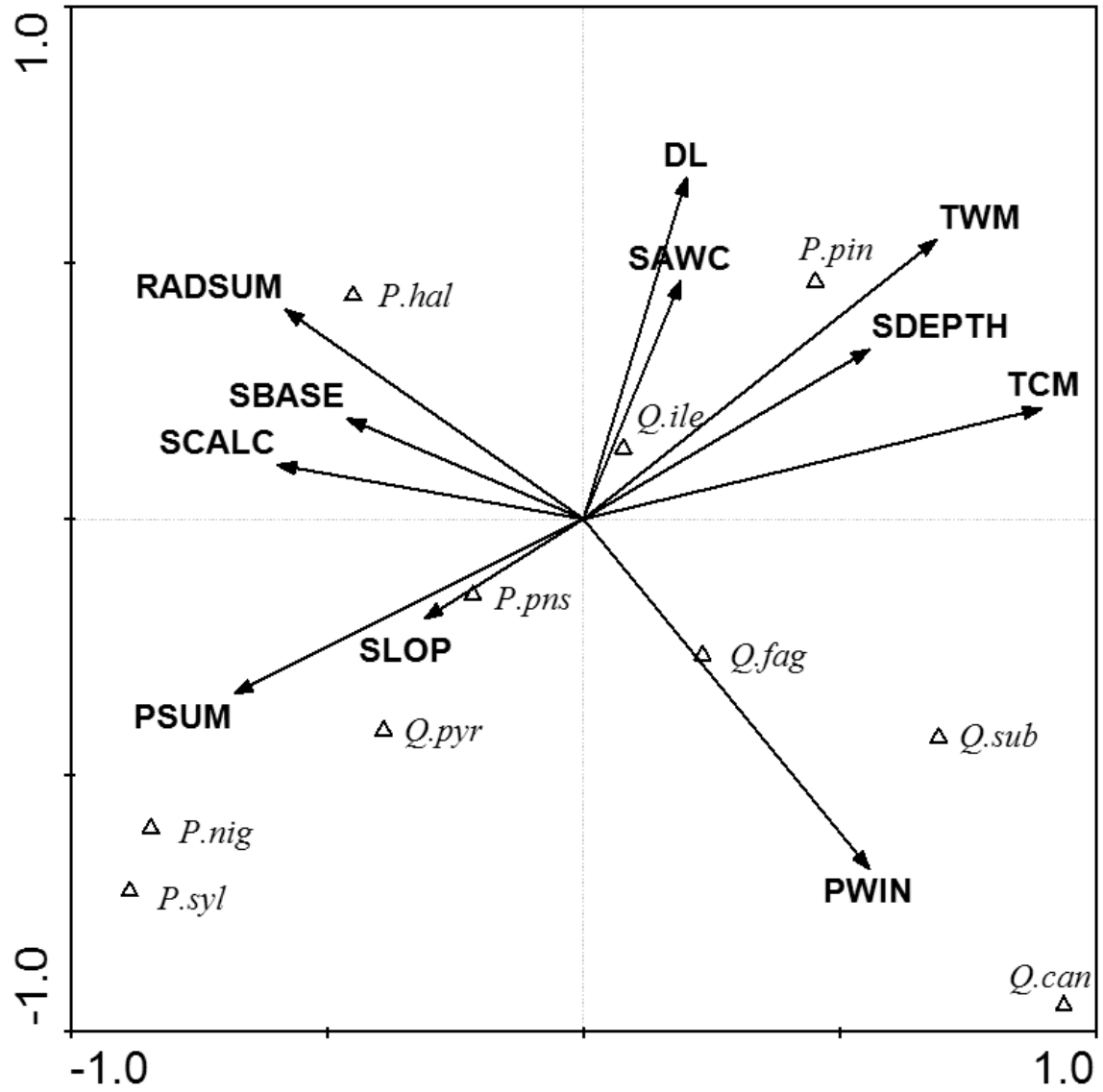

Figure 2.2 CCA biplot of environmental variables in relation to five *Quercus* and *Pinus* species distribution on Axes 1 and 2 (see main text for abbreviations).

Table 2.2 Sequential analyses carried out for variance partitioning calculation. The sum of all eigenvalues (trace), the percentage of the community variance explained and the model significance (by Monte Carlo test) are shown for each analysis.

Analysis (#)	*Independent set*	*Covariable set*	*Trace*	*p (trace)*	*% variance*
DCA (1)	-	-	7.95	-	100
CCA (2)	Environmental	-	1.35	< 0.001	17.0
CCA (3)	Spatial	-	1.31	< 0.001	16.5
pCCA (4)	Environmental	Spatial	0.50	< 0.001	6.3
pCCA (5)	Spatial	Environmental	0.46	< 0.001	5.7

According to GLZ models, which provided a description of the environmental (realized) distribution niche of tree species, *Pinus* and *Quercus* species segregated along Axis 1 (Fig. 2.2), with oaks located towards positives values of the gradient (with the exception of *Q. pyrenaica* and the extreme of *Q. ilex*'s niche) and pines towards the negative side (with the exception of *P. pinea*). This way, the species sequence found from negative to positive values of Axis 1, i.e., from high-steep cold areas, to lower areas with milder climatic conditions was: *Q. pyrenaica*, *Q.ilex*, *Q.faginea*, *Q. suber*, and *Q.canariensis* for oaks (Fig. 2.3a), and *P. sylvestris*, *P. nigra*, *P. halepensis*, *P. pinaster*, and *P. pinea* for pines (Fig. 2.3b). Axis 2 stressed the differences between certain species; *P. pinea* and *P. halepensis* were located at the driest part of the gradient, and *Q. ilex* differed from the rest of oaks reaching drier areas, with lower winter precipitation, longer drought period but under deeper soils with higher water retention capacity (Fig. 2.2).

P. nigra and *P. sylvestris* showed similarities and narrow niches, associated with high elevation, steep slopes, shallow soils, low temperatures, and high values of summer precipitation probably caused by the effect of the orography (Fig. 2.2). At high and steep habitats *Q. pyrenaica* was found, followed by *P. pinaster* and *Q. ilex*, which showed a broader niche amplitude at intermediate conditions. Conversely, *P. pinea* was clearly associated to low elevation warmer areas and deeper soils, and *P. halepensis* in areas with high summer radiation and basic soils with high base saturation and calcium content. *Q. suber* and *Q. canariensis* were restricted to areas with high winter precipitation, mild temperature conditions, shorter drought length, and low calcium soil content. Towards more arid conditions (less winter rain, higher drought and summer radiation), and soils with higher calcium content and base saturation, *Q. faginea* and *Q. ilex* were found. All environmental variables that entered the CCA model provided a significant fit when tested singly to explain species abundance. Overall, environmental variables associated to Axis 1 such as the mean temperature of the warmest and coldest months, explained best the differences between pines (Fig. 2.3d); whereas variables correlated with Axis 2, such as winter precipitation, described oaks segregation at regional scale (Fig. 2.3c).

Quercus and *Pinus* forest regeneration

Adult/regeneration proportion found for each species in SSFI plots have been summarized in Figure 2.4. A high percentage of pine and oak forests showed a limited regeneration (i.e., lack of individuals with a diameter = 7.4 cm). For the five pine species, around 40-55 % of the SSFI plots (with presence of the species) were mature stands with adults (i.e., individuals with a dbh = 7.4 cm) but without saplings or seedlings (i.e., advance regeneration) in the understorey.

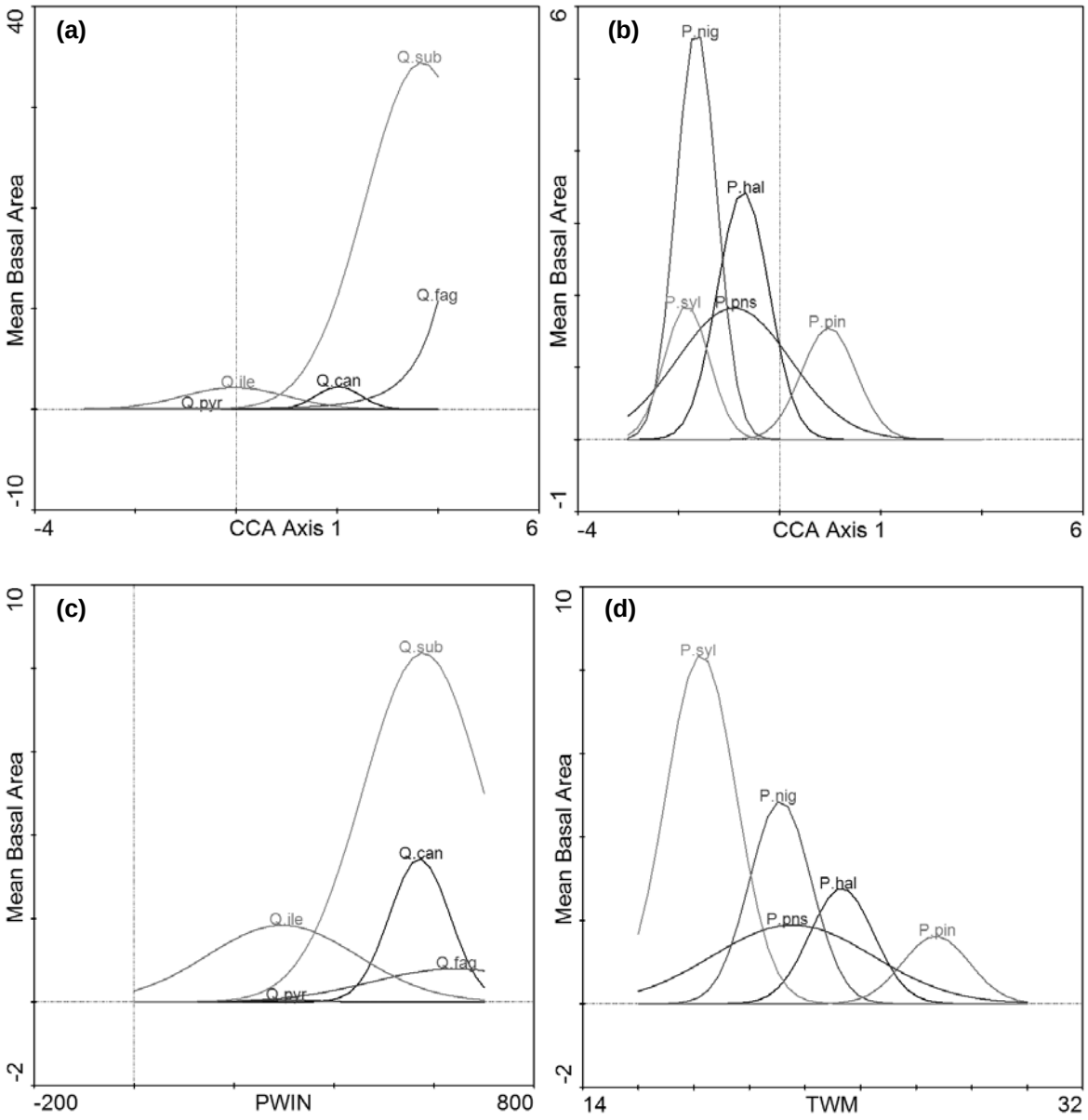

Figure 2.3 *Quercus* (a) and *Pinus* (b) species abundance (mean basal area, m^2/ha) variation along the CCA Axis 1, which is positively correlated with the temperature of the coldest and warmest months, and soil depth; and negatively correlated with summer precipitation, radiation, slope, soil calcium content and soil base saturation. Distribution of *Quercus* (c) and *Pinus* (d) species along the gradients of the temperature of the warmest month (ºC) and mean winter precipitation (mm), respectively.

Among oaks, the percentage of forest stands with limited regeneration varied between species, from 60-70 % of plots for *Q. suber* and *Q. canariensis*, followed by *Q. ilex* and *Q. faginea* (30-40 %) and *Q. pyrenaica* (approximately 25 %) (Fig. 2.4).

Pines' regeneration occurred mainly under the canopy of pine forests, with proportions (from total SSFI plots of species) ranging from 15-20 % for *P. pinea* and *P. pinaster*, to 30-40 % for *P. sylvestris*, *P. nigra*, and *P. halepensis*. Regeneration under the canopy of oak forests for all five pine species was scarce, with less than 10% of plots per species. The remaining plots included pine regeneration in areas with no canopy (i.e., sampled plots with no tree layer but potentially with shrubby vegetation, where pine "colonization" might be occurring), with *P. pinea* (25%), *P. halepensis* (20%), and *P. pinaster* (15%) showing a significant proportion (Fig. 2.4). On the contrary, oaks that showed some regeneration, such as *Q. faginea* and *Q. ilex*, had as much regeneration under their own canopy as under pine forests: (around 30% for *Q. faginea*), or even a greater proportion under pines (30%) than under oaks (15%) in the case of *Q. ilex* (Fig. 2.4). The scarce regeneration of *Q. canariensis* (30% in total) was found mainly under its own canopy. *Q. suber* showed similarly low regeneration under its own canopy than in forest areas with no tree layer (approximately 10% in each). *Q. pyrenaica* and *Q. ilex* also showed a significant proportion (20-25 %) of plots in areas outside forest stands with no canopy.

Adults *versus* regeneration distribution patterns

The abundance of pine and oak regeneration and adults was plotted in the bi-dimensional environmental region defined by the first two CCA axes (Fig. 2.5). Highly significant unimodal models showed that pines had overall closely associated distribution areas between their adults and regeneration. Conversely, some oak species diverged in the environmental conditions under which both stages, adult trees and regeneration, were found as inferred from their non- overlapping 95% confidence intervals. Specifically, *Q. pyrenaica* tended to regenerate in areas slightly different from its adults, with lower summer precipitation, higher mean temperatures of the coldest and warmest months, and smoother relief (Fig. 2.5). *Q. faginea*'s regeneration niche was characterized by conditions under lower winter precipitation, higher summer radiation and greater calcium soil content than those found for *Q. faginea* adult trees.

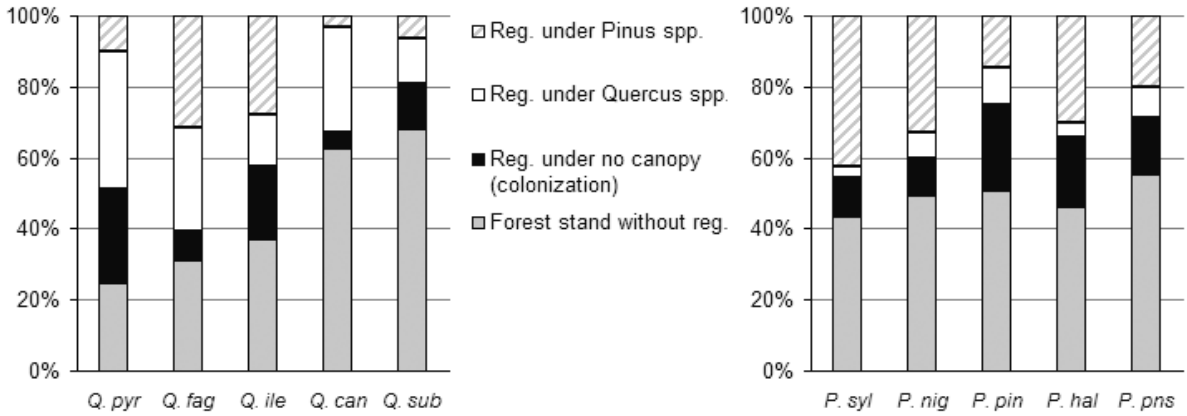

Figure 2.4 Adult and regeneration proportion found in SSFI plots for *Quercus* (left) and *Pinus* (right) species. The type of habitat in which species regeneration occurs is specified, i.e., under the canopy of *Pinus* or *Quercus*, or treeless forest areas. Percentages are referred to the total number of plots each species was found (see Fig 2.1).

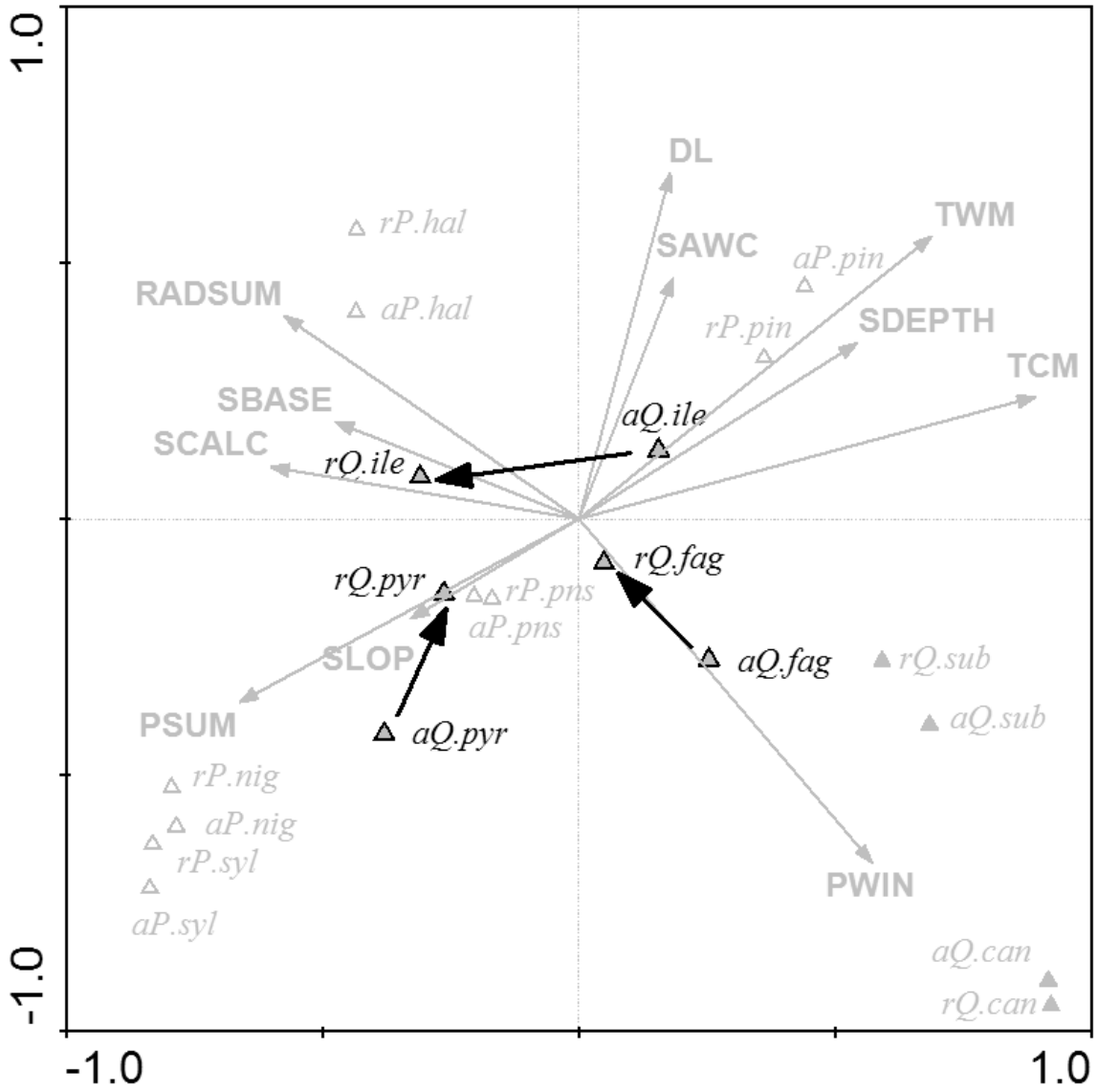

Figure 2.5 CCA biplot of environmental variables, analogous to Fig. 2.2, but showing the centroid for regeneration "r" and adults "a" of *Quercus* and *Pinus* species. For the three species highlighted, *Q. ilex*, *Q. faginea* and *Q. pyrenaica*, adult and regeneration distribution are far apart, with no overlap in their confidence intervals (not shown for better visualization). See the main text for abbreviations.

Similarly, *Q. ilex* regeneration was found in colder areas, with higher summer radiation, and clearly associated to high levels of base saturation and calcium content in the soil compared to adults (Fig. 2.5). Results of stepwise partial CCA (differentiating regeneration and adults) but constrained by environmental variables and using the best spatial predictors as covariables (i.e., analysis labelled as (4) in Table 2.2) showed the same global distribution pattern of species. However, the differential distribution found between adults and regeneration got slightly reduced, especially for *Q. ilex*, in which the spatial structure of data might be exerting some influence in the distribution patterns described.

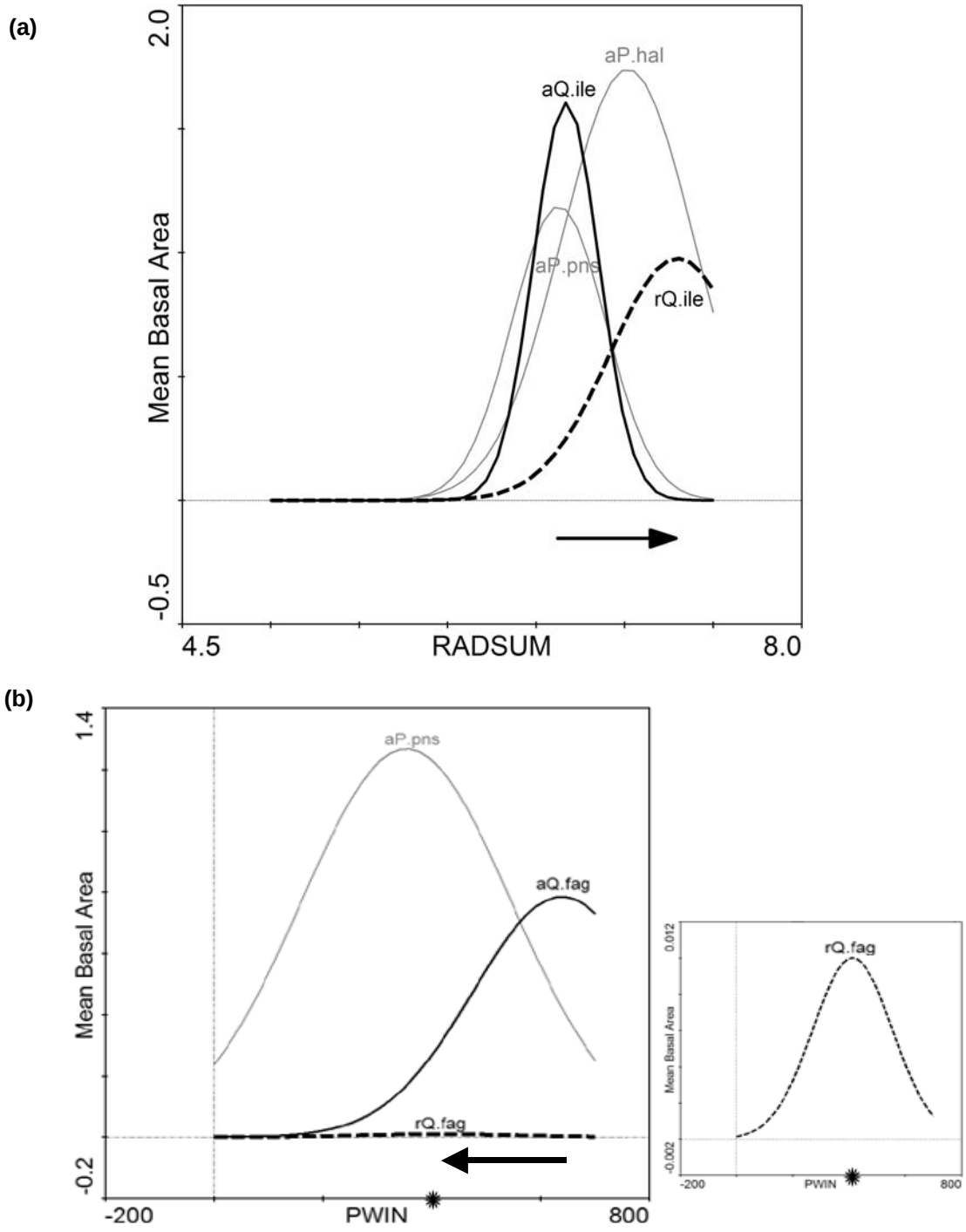

Figure 2.6 *Q. ilex* (a) and *Q. faginea* (b) adult's distribution (black line) and regeneration niche (dotted line) along the summer radiation (kwh/m^2) gradient and winter precipitation gradient (mm), respectively. *Pinus* species distribution along the gradients is represented in grey lines. Both *Quercus* species show the maximum of the regeneration curves displaced towards more arid areas under the canopy of pines. A zoom has been made in (b) to the regeneration curve of *Q. faginea* for a better visualization with the asterisk as reference for comparison (notice different scales).

Since *Q. ilex* and *Q. faginea* regeneration had been found to be substantial under pines' canopy (see Fig. 2.4), we explored possible interaction of both oak species with pines along the main environmental gradients. *Q. ilex* adults and regeneration distribution differed substantially along the summer radiation gradient. *Q. ilex* regeneration was displaced toward positive values of the gradient, reaching areas with higher radiation where *Q. ilex* forest stands (adult trees) were not present. More interestingly, *Q. ilex* regeneration occurred principally under the canopy of *P. pinaster* and *P. halepensis* (Fig. 2.6a). Likewise, the same pattern was found along the gradient of temperature of the coldest month, where *Q. ilex* regenerated in the coldest areas mainly under *P. halepensis* canopy (figure not shown). *Q. faginea* showed the same proportion of regeneration under pines than under its own canopy. Along the gradient of mean winter precipitation, regeneration niche was found at drier areas (with 400 mm mean rainfall) than *Q. faginea* adults (around 700 mm). Furthermore, at the driest part of the gradient *Q. faginea* regeneration occurred mainly under the canopy of *P. pinaster* (Fig. 2.6b).

Discussion

Broad scale vegetation controls: climate and soil influence

Results evidence a primary importance of climate in explaining pine and oak species abundance at regional scale in Andalusia, and a secondary (but key for some species) relevance of substrate (soil characteristics) and microclimate (topography). Low winter temperatures and water stress have been considered to exert influence on many features of the flora in the Mediterranean region (Mitrakos 1980). Pine and oak species segregate along altitudinal gradients that often correlate with the variability in resources (e.g., water availability) or environmental condition (e.g., temperature or radiation). Overall, pines were found in habitats with colder conditions and at highest altitudes than oaks. The abundance distribution of oaks was explained by a water availability gradient, i.e. winter precipitation. Thus, we confirmed the importance of temperature (for pines) and precipitation regime (for oaks) in controlling species abundance patterns at a regional scale, as found in previous studies (Rouget *et al.* 2001; Thuiller *et al.* 2003). Soil factors were key for some species such as *Q. suber* and *Q. canariensis* which were associated to acidic, non-calcareous soils, and for *P. halepensis*, frequently located on calcareous soils.

Studied species exhibit quite different life history and ecophysiological strategies (see Sánchez-Gómez *et al.* 2006a; Valladares and Sánchez-Gómez 2006), which could partly explain their differential distribution. The temperature gradient exerts an important influence on pine species distribution (Morin *et al.* 2007). We found that a gradient from high-steep cold areas to lower areas with milder climatic conditions, explained the differential distribution between pines, with *P. sylvestris* and *P. nigra* in the coldest extreme (see Castro *et al.* 2004), followed by *P. halepensis* and *P. pinea* in milder environments, and *P. pinaster* tolerating a wider range of conditions.

Among Mediterranean oaks, different strategies in response to drought may contribute to explain species differences in productivity, competitive ability and distribution patterns along aridity gradients (Salleo and Lo Gullo 1990; Acherar and Rambal 1992), which appear to be controlled by their differential leaf habit and tissue water relationships (Villar-Salvador *et al.* 1997; Castro-Díez *et al.* 1998; Quero *et al.* 2006). Our results showed evergreens (especially *Q. ilex*) reaching drier conditions than deciduous oaks. Under water stress the low cell-wall elasticity of evergreens allow them a rapid recovery after a decrease in soil water content, whereas the elastic cell walls of the deciduous oaks would experience a greater water loss in leaves than those of evergreens (Corcuera *et al.* 2002). *Q. faginea* shows a higher stomatal conductance and requires higher water availability to simultaneously increase

growth and storage than *Q. ilex* (Sanz-Pérez *et al.* 2007); thus, the former could be classified as a water-spending species while the later as a drought-avoiding species (Mediavilla *et al.* 2004). Furthermore, under mild freezing conditions common in winter, the maintenance of both photosynthetic and vascular function allows the evergreen species to continue photosynthesis and gas exchange throughout the winter, providing and advantage over their deciduous congeners, which show a higher sensitivity to freezing in leaves and xylem (Cavender-Bares *et al.* 2005). *Q. ilex*, the species with the longest leaf lifespan and narrowest vessel diameters, shows the highest drought and freezing tolerance, which could explain its ability to inhabit a broader range of conditions in Andalusia.

Given the regional scale of the study, the spatial structure detected in species data is mainly related to the strong spatial structure of the main conditioning environmental factors, as the climatic ones. On the contrary, in small spatial scale studies we have found that most of the explained spatially structured variance is related to community-based processes, instead to spatially structured environmental variation (Maltez-Mouro *et al.* 2005, 2007). Furthermore, current distribution of some Mediterranean species is strongly influenced by land use history and current management. For example, *Pinus* and *Quercus* species distribution patterns in North-eastern Iberian Peninsula show a shifting mosaic in stand composition of pines and oaks along disturbance and aridity gradients (Retana *et al.* 1996; Zavala 1999). SSFI sampling favoured abundant species and scarce species are likely to have been under-sampled (e.g., *P. sylvestris*, *Q. pyrenaica*). Although fire frequency did not come to be a significant factor in the models, probably due to the type of variable used in the analyses, it also plays a crucial role in Mediterranean landscapes (Pausas *et al.* 2004a; Broncano *et al.* 2005), together with other factors not recorded here, such as dispersal limitation (Purves *et al.* 2007) or human disturbances (Plieninger *et al.* 2003; Urbieta *et al.* in press), which can alter species-environment correlation (see Pacala and Hurtt 1993; Purves *et al.* 2007).

Pine and oak forest regeneration and stand dynamics

Inventory data revealed that a high percentage of pine and oak forests showed limited regeneration, specially remarkable in the case of *Q. suber* and *Q. canariensis* stands, which emphasize the importance of these species to be included in restoration and conservation plans. Pines' regeneration occurred mainly under the canopy of pine forests, and significantly in forest areas with no tree canopy. Conversely, oaks showed as much regeneration under their own canopy as under pine forests (for *Q. faginea*), or even a greater proportion under the canopy of pines (for *Q. ilex*). These findings support other studies in different regions which reported evidence of pines regenerating mostly in pine-dominated fragments or open areas, and oaks showing highest regeneration in pine dominated stands (Galindo-Jaimes *et al.* 2002).

It is well established that many pine species can germinate and establish successfully in open areas (Broncano *et al.* 1998; González-Espinosa *et al.* 1991), due to their wind dispersed seeds, and their ability to survive and maintain high plant growth in open habitats (Valladares and Sánchez-Gómez 2006), which allow them to become successful invaders (Richardson and Bond 1991). Pines are likely to persist in frequently disturbed stands, thanks to their effective post-fire regeneration (Pausas *et al.* 2003; Broncano *et al.* 2005) or under stressful, i.e. xeric, conditions (Zavala and Zea 2004). Radiation intensity and water stress diminish and can facilitate subsequent oak establishment (Retana *et al.* 1999), which survive better under moderate radiation conditions (Espelta *et al.* 1995; Rey Benayas 1998), such as those found under the canopy of pine forests (Lookingbill and Zavala 2000). At the long run oak saplings might survive under pine canopy due to their greater tolerance to shade (Sánchez-Gómez *et al.* 2006b).

Niche expansion of oaks by facilitation

Many plants modify the local environment and facilitate neighbouring plants of different species simply through their presence, especially in areas with abiotic stress such as the Mediterranean (Bertness and Callaway 1994; Gómez- Aparicio *et al.* 2004). Facilitative interactions may lead to a species' realized niche being larger than its fundamental niche, and might promote the expansion of a species' range margin into more severe environmental conditions than would otherwise be tolerable (Bruno *et al.* 2003). Since high radiation levels lead to increased temperature and high water evaporation rates, germination of many Mediterranean species is expected to be favoured under some degree of canopy closure (Bran *et al.* 1990; Espelta *et al.* 1995). Fore example, high radiation levels exert a negative effect on oak seedlings as shown experimentally by Valladares *et al.* (2000).

Our results show that a high proportion of the forest regeneration for *Q. ilex* and *Q. faginea* occurs under the canopy of pines, particularly in areas with increasing environmental severity, i.e., in the coldest and more arid extremes of the environmental gradients explored. This suggests a possible facilitative effect of pines on the establishment of oak species. The consequences of the forest regeneration patterns described in this study for stand dynamics support the evidences that an eventual replacement of pines by oaks may occur as predicted in other areas (see Zavala and Zea 2004). The improvement in soil fertility and microclimate provided by *P. halepensis* canopy is known to facilitate the establishment of perennial grasses and shrubs (Maestre *et al.* 2004; Arrieta and Suárez 2006), but negative effects on species richness and plant establishment in the understorey have also been reported (Bellot *et al.* 2004). Thus, the suitability of pine forests on spontaneous vegetation establishment is still an open debate (see Maestre *et al.* 2004). Improved understanding of forest structure and facilitation processes along environmental gradients has direct relevance for the development of tools for ecosystem restoration, and for anticipating the response of plant species and communities to key environmental change drivers.

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Appendix 2.1

Principal dominant soil typological units in Andalusia, named according to the FAO-UNESCO soil legend, and derived from the soil geographical database of Europe (scale 1/1000000) (European Soil Bureau 1999). The number of SSFI plots found in each soil type are summarized.

F.A.O. (1974, act)	# SSFI plots
Eutric Planosol	23
Gypsic Xerosol	8
Gleyic Solonchak	0
Rhodo-Chromo-Calcic Luvisol	3
Pellic Vertisol	36
Calcic Xerosol	39
Dystric Lithosol	188
Calcaric Fluvisol	121
Gleyic Acrisol	51
Luvic Arenosol	506
Calcaric Lithosol	223
Rhoso-Chromic Luvisol	123
Chromic Vertisol	299
Eutric Cambisol	1297
Rendzina	1126
Humic Cambisol	605
Calcic Cambisol	3239
Dystric Regosol	1245
Eutric Regosol	3415
MISSING	25
TOTAL	**12572**

Appendix 2.2

Tables with environmental characteristics of *Quercus* and *Pinus* species distribution range in each of the originally selected environmental variables. See the main text for abbreviations and units.

	Q. ilex (n=6428)				***Q. suber (n=2001)***				***Q. faginea (n=964)***			
Variable	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			105,948	596,000			113,799	494,000			140,068	577,000
UTMY			4,036,000	4,287,000			3,994,000	4,255,000			3,996,000	4,262,000
ALTI	755	432	10	1938	408	222	4	1280	783	384	45	1780
SLOP	13	10	0	53	13	9	0	45	17	9	0	45
SN	0.0	0.7	-1.0	1.0	0.0	0.7	-1.0	1.0	0.2	0.7	-1.0	1.0
PANU	667	167	268	1366	838	182	489	1366	800	175	350	1315
PSPR	177	48	71	356	198	39	111	338	216	56	97	356
PSUM	39	15	13	90	29	9	14	53	45	19	16	85
PAUT	190	41	96	357	241	49	145	355	218	44	108	344
PWIN	262	83	83	655	373	98	186	655	323	88	99	596
TPET	781	79	525	938	827	41	677	929	767	67	557	901
TSUP	341	150	18	1039	484	167	172	1039	465	160	76	970
TDEF	454	70	277	634	471	48	371	601	430	68	289	567
DL	5.1	0.7	4	8	5.0	0.5	4	8	4.7	0.5	4	7
RADANU	4.5	0.1	4.2	4.7	4.4	0.1	4.1	4.6	4.4	0.1	4.1	4.7
RADSUM	6.7	0.1	6.1	7.1	6.5	0.2	5.4	6.9	6.6	0.1	6.2	7.0
TANU	14.8	2.1	7.6	18.3	16.4	1.0	12.3	18.3	14.5	1.9	8.4	18.0
TWM	24.6	1.9	17.9	28.4	25.1	1.1	21.4	27.3	24.4	1.6	18.8	27.3
TCM	6.9	2.1	0.2	11.6	9.3	1.6	5.0	12.5	6.7	2.2	0.9	12.3
TOSCI	17.7	1.4	13.7	20.5	15.8	2.0	12.2	20.4	17.7	1.9	12.2	20.5
SAWC	127.3	48.5	12.0	220.0	120.6	48.0	16.5	220.0	113.2	47.9	12.0	220.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	3	0	1	3	3	2	1	3	3	0	1	3
SCALC	1	2	1	3	1	0	1	3	2	2	1	3
SDEPTH	3	0	1	3	3	0	1	3	3	0	1	3
FIRE (**)	215 (3.3 %)				119 (6.0 %)				29 (3.0 %)			

(*) Median, Quartile range (Q3-Q1), Maximum, Minimum

(**) Number and percentage of SSFI plots that have suffered a fire between 1987-2002

	Q. canariensis (n=300)				*Q. pyrenaica (n=49)*			
Variable	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			172,293	366,000			175,418	538,000
UTMY			4,012,000	4,246,000			4,077,000	4,250,000
ALTI	431	206	34	1346	1246	415	538	1926
SLOP	16	8	0	45	18	10	0	45
SN	0.2	0.7	-1.0	1.0	0.0	0.7	-1.0	1.0
PANU	1073	111	628	1338	770	121	603	990
PSPR	249	30	140	332	198	33	148	283
PSUM	27	5	18	49	43	13	26	82
PAUT	304	28	170	352	218	30	165	278
PWIN	496	53	232	638	312	60	216	426
TPET	798	33	661	876	695	83	537	797
TSUP	703	107	298	1011	459	90	290	609
TDEF	424	27	351	520	384	48	303	462
DL	4.8	0.4	4	5	4.7	0.5	4	5
RADANU	4.3	0.1	4.1	4.5	4.5	0.1	4.3	4.6
RADSUM	6.3	0.1	6.2	6.7	6.7	0.1	6.5	6.8
TANU	16.0	0.9	11.7	18.0	12.4	2.5	7.9	15.6
TWM	24.1	0.6	20.8	25.8	22.3	2.3	18.3	25.8
TCM	9.6	1.2	5.2	12.3	4.9	2.5	0.4	8.2
TOSCI	14.5	0.9	12.7	19.1	17.4	1.1	15.4	20.4
SAWC	79.0	36.5	16.5	220.0	129.6	46.7	63.5	165.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	1	2	1	3	3	0	1	3
SCALC	1	0	1	3	1	2	1	3
SDEPTH	3	0	1	3	3	0	1	3
FIRE (**)	5 (1.6%)				1 (2.0%)			

	P. halepensis (n=1972)				***P. pinaster (n=1781)***				***P. pinea (n=1495)***			
Variable	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			162,673	597,000			110,800	583,000			108,905	544,000
UTMY			4,008,000	4,261,000			4,002,000	4,262,000			3,995,000	4,261,000
ALTI	946	301	20	1666	918	416	5	1958	362	268	0	1426
SLOP	18	10	0	53	18	9	0	49	10	9	0	41
SN	0.0	0.7	-1.0	1.0	0.0	0.7	-1.0	1.0	-0.1	0.7	-1.0	1.0
PANU	557	187	212	1363	723	191	308	1361	633	96	350	1321
PSPR	154	57	57	355	193	56	82	356	156	26	96	333
PSUM	39	16	11	86	41	17	12	84	29	11	12	78
PAUT	161	43	71	357	203	50	90	356	183	28	116	345
PWIN	202	88	62	654	286	97	91	654	265	50	108	606
TPET	738	51	623	915	748	72	525	919	855	43	674	929
TSUP	248	167	0	1033	397	169	41	1033	301	87	76	980
TDEF	429	56	15	673	422	64	288	603	521	50	1	603
DL	5.6	1.2	1	11	4.9	0.7	4	8	5.6	1.1	1	8
RADANU	4.5	0.1	4.2	4.7	4.5	0.1	4.1	4.7	4.4	0.1	4.1	4.7
RADSUM	6.7	0.1	5.8	7.1	6.6	0.1	5.9	7.1	6.5	0.2	5.3	6.9
TANU	13.9	1.5	10.3	18.4	14.0	2.0	7.6	18.3	16.7	1.2	11.7	18.4
TWM	23.6	1.2	20.3	27.5	23.8	1.9	17.9	27.9	26.0	0.8	21.3	27.9
TCM	6.3	1.8	2.4	12.0	6.4	2.2	0.2	12.0	8.9	1.8	3.6	12.3
TOSCI	17.3	1.4	12.6	20.2	17.4	1.7	12.4	20.4	17.1	2.1	12.2	20.4
SAWC	122.4	52.6	12.0	220.0	113	50.6	12.0	220.0	132	41.9	63.5	220.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	3	0	1	3	3	0	1	3	3	1	1	3
SCALC	3	0	1	3	1	2	1	3	1	1	1	3
SDEPTH	3	0	1	3	3	0	1	3	3	0	1	3
FIRE*	96 (4.8%)				152 (8.5%)				63 (4.2 %)			

(*) Median, Quartile range (Q3-Q1), Maximum, Minimum

(**) Number and percentage of SSFI plots that have suffered a fire between 1987-2002

	P. nigra (n=991)				*P. sylvestris (n=291)*			
Variable	Mean	SD	Min.	Max.	Mean	SD	Min.	Max.
UTMX			127,364	583,000			318,000	578,000
UTMY			4,061,000	4,249,000			4,063,000	4,239,000
ALTI	1492	256	41	2305	1807	215	1214	2309
SLOP	18	9	0	53	17	7	0	42
SN	0.1	0.7	-1.0	1.0	0.1	0.7	-1.0	1.0
PANU	715	211	347	1129	562	102	391	1066
PSPR	213	71	97	356	156	25	111	330
PSUM	59	19	15	90	42	7	25	78
PAUT	192	39	108	280	170	28	110	278
PWIN	252	89	88	437	195	54	106	417
TPET	656	32	525	896	625	33	523	715
TSUP	398	193	50	791	275	104	86	713
TDEF	338	30	277	565	336	27	276	415
DL	4.5	0.6	4	8	4.9	0.4	4	6
RADANU	4.5	0.1	4.3	4.7	4.6	0.1	4.3	4.6
RADSUM	6.7	0.1	6.4	6.9	6.7	0.0	6.5	6.8
TANU	11.3	1.0	7.6	18.0	10.3	1.1	7.3	13.5
TWM	21.6	1.1	17.9	26.3	20.1	1.1	17.4	23.2
TCM	3.6	1.0	0.2	10.9	3.2	1.0	-0.1	6.6
TOSCI	18.0	1.0	15.0	19.4	16.9	0.7	15.2	19.0
SAWC	76.2	44.6	12.0	165.0	64.5	46.4	12.0	165.0
Variable (*)	Median	Quart.	Min.	Max.	Median	Quart.	Min.	Max.
SBASE	3	0	1	3	3	0	1	3
SCALC	3	0	1	3	1	2	1	3
SDEPTH	2	1	1	3	3	2	1	3
FIRE*	11 (1.1%)				7 (2.4%)			

Capítulo 3

Capítulo 3

Factores ambientales y antrópicos como determinantes de la composición de los bosques del sur de la Península Ibérica: hacia un predominio del alcornoque debido al manejo forestal del siglo XX

Este capítulo reproduce el texto del siguiente manuscrito:

Urbieta, I.R., Zavala, M.A. and Marañón, T. Human and non-human determinants of forest composition in southern Iberian Peninsula: evidence of shifts toward cork oak dominance due to management over the past century. Journal of Biogeography (in press).

Resumen

Tanto factores ambientales como factores humanos han configurado la estructura de los bosques mediterráneos durante milenios. Sin embargo, no se conoce con profundidad la influencia que las actividades humanas más recientes han ejercido en la composición actual de los bosques. En este estudio se han cuantificado los cambios ocurridos durante el último siglo en la composición de los bosques mixtos de *Quercus suber* L. (alcornoque) y *Q. canariensis* Willd. (quejigo moruno) de las sierras al norte del estrecho de Gibraltar. Se examinaron los efectos del manejo forestal y de los factores ambientales (clima, topografía) en la estructura de los bosques a diferentes escalas espaciales y temporales. En primer lugar, se analizaron los cambios en la composición de especies en nueve bosques mixtos (~ 40.000 ha) a partir de los datos de las series de inventarios forestales realizados a lo largo del último siglo, teniendo en cuenta los cambios en las condiciones ambientales y la gestión forestal de ese periodo. En segundo lugar, se analizó la estructura actual de las masas de *Q. suber- Q. canariensis* a lo largo de gradientes ambientales a dos escalas espaciales: (1) a escala de paisaje (~ 284 ha), combinando inventarios locales y variables topográficas derivadas de un modelo digital del terreno, y (2) a escala regional (~ 87.600 km^2), combinando los datos del Segundo Inventario Forestal Nacional para Andalucía con estimaciones de variables climáticas. Los datos históricos mostraron cambios en la composición de los bosques debido a la influencia humana, con un rápido incremento en la densidad de alcornoques a lo largo del siglo pasado. La selvicultura ha favorecido al alcornoque (para la producción de corcho) a expensas del quejigo, lo que ha determinado en gran medida la estructura actual de los bosques mixtos. La abundancia de las dos especies es mayor a medida que aumenta la precipitación media anual, y coexisten a partir de los 800 mm (límite inferior para el quejigo). A pesar de que el alcornoque domina en la mayoría de los rodales, la red de drenaje condiciona la distribución diferencial de las dos especies en el paisaje, con los quejigares claramente asociados a los hábitats más húmedos cercanos a los cursos de agua. En lo relativo al papel de la gestión forestal, este estudio ilustra y cuantifica un ejemplo reciente de cambio en la composición de los bosques mediado por las actividades humanas. El nicho realizado del alcornoque ha sido ampliado a expensas del quejigo, lo que apoya las evidencias de que los seres humanos han inducido fuertes cambios en la composición de los bosques de *Quercus* en la cuenca mediterránea. No obstante, los recientes problemas de regeneración detectados en los rodales de alcornoque, la menor demanda de productos forestales, las nuevas políticas de conservación y el cambio climático auguran nuevos cambios en la composición de estos bosques.

Human and non-human determinants of forest composition in southern Iberian Peninsula: evidence of shifts toward cork oak dominance due to management over the past century

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Abstract

Both human and non-human determinants have shaped Mediterranean forest structure over millennia. The effects of recent human activities on forest composition, however, remains poorly understood. We quantified forest composition changes during the past century in the mixed forests of *Quercus suber* L. (cork oak) and *Q. canariensis* Willd. (Algerian oak) of the mountains north of the Strait of Gibraltar (S Spain), and explored the effects of forest management and environmental (climate, topography) factors on forest structure at different spatial and temporal scales. First, we quantified 20th century changes in species composition from a series of inventories in nine mixed forests (~ 40000 ha), and discussed them in terms of the management practices and environmental conditions. Second, we analysed present-day *Q. suber* and *Q. canariensis* stand structure along environmental gradients at two spatial scales: (1) that of the forest landscape (~ 284 ha), combining local inventories and topographic variables, using a digital elevation model, and (2) regional (~ 87600 km^2), combining data from the Spanish Forest Inventory for the Andalusia region and estimates of climatic variables. Historical data indicate anthropogenic changes in stand composition, revealing a sharp increase in the density of cork oaks over the last century. Forest management has favoured this species (for cork production) at the expense of *Q. canariensis*. The impact of management is imprinted on the present-day forest structure. The abundance of both species increases with annual mean precipitation, and they coexist above 800 mm (the minimum threshold for *Q. canariensis*). *Q. suber* dominates in most of the stands, and species segregation in the landscape is associated with the drainage network, *Q. canariensis* being clearly associated with moister habitats near streams. Our study quantitatively exemplifies a recent human-mediated shift in forest composition. As a result of forest management, the realized niche of the cork oak has been enlarged at the expense of that of *Q. canariensis*, providing further evidence for humans as major drivers of oak forest composition across the Mediterranean. Recent regeneration problems detected in *Q. suber* stands, a lesser demand for wood products, conservation policies, and climate change augur new large-scale shifts in forest composition.

Keywords: Deciduous forest; environmental gradients; forest structure; human impact; land-use history; Mediterranean forest; *Quercus suber*; *Quercus canariensis*; sclerophyllous; Strait of Gibraltar.

Introduction

Contemporary vegetation patterns result from the combination of species' individual responses and interactions along environmental and disturbance gradients (Whittaker and Levin 1977). Furthermore, it is widely recognised that humans have played an important role in modifying and regulating the types and rates of ecosystem change at various spatio-temporal scales (Vitousek *et al*. 1997; Sanderson *et al*. 2002; Haberl *et al*. 2007). Thus, disentangling environmental versus human effects is critical for understanding current vegetation patterns and potential shifts under global change (e.g., Noble and Dirzo 1997; Levin 1999).

Humans have actively modified forest species distributions by deliberately introducing and harvesting selected species and genotypes, but also indirectly through forestry practices that have favoured certain species (e.g., Zobel *et al*. 1987; Crosby 1994; Richardson 1998; Le Maitre 1998; Gil *et al*. 2004). These effects have been particularly marked in regions such as the Mediterranean Basin, with a long history of human settlement, in which anthropogenic disturbances are considered key factors affecting forest structure and composition (Thirgood 1981; Quézel 1985; Blondel and Aronson 1995; Grove and Rackham 2001).

Palynological studies show that forest composition in the Mediterranean region has changed dramatically over the past millennia, including partial replacement of deciduous taxa by sclerophyllous species (Reille and Pons 1992; Blondel and Aronson 1999). For example, in the case of *Quercus* species, the evergreen *Q. ilex* L. and *Q. coccifera* L. appear to have replaced *Q. pubescens* Willd. in large areas of southern France during the last three millennia (Vernet 1973; Pons and Quézel 1985); *Q. ilex* and *Q. suber* L. may have replaced the deciduous *Q. canariensis* Willd. and *Q. pyrenaica* Willd. in northern Morocco (Reille 1977); and *Q. ilex* and *Q. suber* have generally become more abundant at the expense of more mesic tree species in the Iberian Peninsula (Carrión *et al*. 2000). Post-glacial oak distribution changes were strongly correlated with large-scale shifts in the climatic conditions, and subsequently with interspecific competition and landscape topography (Brewer *et al*. 2002; Petit *et al*. 2002). Later changes during the last six millennia were more strongly controlled by human activities, such as the historical use of fire and livestock (Carrión *et al*. 2003). An increase in the impact of human activities would be expected to be seen with the approach of modern times (Hobbs *et al*. 2006), especially since forest management activities have intensified (e.g., Riera-Mora and Esteban-Amat 1994). The effects of more-recent (i.e., 20th century) human activities on forest composition remain, however, very poorly understood, and very few studies provide quantitative evidence of shifts in species composition due to forest management.

In this study, we focused on one of the largest oak forests within the Mediterranean Basin. It is located in the mountains north of the Strait of Gibraltar (Andalusia, southern Iberian Peninsula), and has experienced a long history of human impact. We tracked changes in forest composition over the last century, and analysed current forest structure along environmental (topographic and climatic) gradients. The forests are composed of the evergreen *Q. suber* (cork oak), which covers a wide range of coastal areas in the western Mediterranean, and the deciduous *Q. canariensis* (Algerian oak), which is mainly limited to the mountains on each side of the Strait of Gibraltar, and some patches in Catalonia (NE Iberian Peninsula) and the Algarve (S Portugal) (Costa *et al*. 2005). Palaeobotanical data of the study area -the Strait of Gibraltar- reveals human presence since the Palaeolithic, and a highly diversified landscape (including oak, pine, juniper and mixed woodlands), which suffered few changes during climatic fluctuations, and acted as a bio-

diversity refuge (Finlayson and Carrión 2007; Carrión *et al*. in press). More-recent palynological records show that deciduous oaks were dominant in northern Moroccan mountains from the end of the Boreal stage (about 7500 years B.P.) until a shift to the evergreens *Q. ilex* and *Q. suber*, associated with human colonisation and partial deforestation for agriculture (Reille 1977; Lamb *et al*. 1991). Modern forest management practices may have continued favouring species such as *Q. suber* (for agrosilvopastoral systems and cork harvesting) at the expense of other trees, particularly after the cork industry developed in the nineteenth century.

We followed a hierarchical approach to analyse patterns and factors operating at different scales (Willis and Whittaker 2002; Pearson and Dawson 2003) in order to disentangle the relative contribution of human and non-human determinants in shaping current forest structure. At a landscape scale, we analysed a sequence of forest inventories and historical records of temperature and precipitation to investigate the role that human management and recent changes in climatic conditions may have played in shaping mixed *Q. suber*-*Q. canariensis* forest composition over the past century. Furthermore, we targeted a mixed forest to examine present-day patterns of segregation and co-occurrence of the two species in relation to topography (aspect, drainage) and distance to roads (access-cost).

At a regional scale, we analysed the distribution of the two oak species along climatic gradients. Species-specific maximum-likelihood models relating species abundance to environmental variables (at both landscape and regional scales) were formulated to explore the main factors controlling stand structure. We addressed the following questions: (1) What are the main factors that have shaped current mixed *Q. suber* and *Q. canariensis* forest structure? (2) Has forest management over the past century driven major changes in stand composition -in particular, have silvicultural practices resulted in shifting dominance of sclerophyllous cork oak versus deciduous *Q. canariensis* in mixed oak forests? (3) How does present-day stand structure vary along environmental and management gradients at landscape and regional scales? (4) Have historical factors left an imprint on current forest composition?

Material and methods

Study area

The study area is located in Andalusia (a region of 87600 km^2 in southern Iberian Peninsula), which is bordered by the Atlantic Ocean (on the south-west) and the Mediterranean Sea (on the south-east) (Fig. 3.1a). *Q. suber* is widely distributed in this region (Fig. 3.1b), where it is found in more than 15% (n=1983) of the Spanish Second Forest Inventory (SSFI) plots, showing a high proportion (42%) of monospecific stands. Its distribution area extends from west to east in the mountains north of the Guadalquivir fault, and in the southern mountains near the Strait of Gibraltar. It is not found in the most arid eastern areas and has been almost eliminated by agricultural transformation of the Guadalquivir river valley. In contrast, *Q. canariensis* has a smaller distribution area (Fig. 3.1c), and is found in just 2.3% (n=300) of SSFI plots in Andalusia, mainly in the elevations close to the Strait of Gibraltar. Within the distribution area of *Q. canariensis*, mixed stands of the two oaks are frequent; i.e., in 80% of *Q. canariensis* SSFI plots, it co-occurred with *Q. suber*.

The analysis of historical changes in forest composition and of species distribution at the landscape scale was focused on forests of the Aljibe Mountains (northern side of the Strait of Gibraltar), where the two oaks form a mixed woodland of about 1700 km^2, protected within Los Alcornocales (the Spanish term for: "cork oak woodland") Natural Park (see Figs. 3.1, 3.3). This area is part of the Betic-Riffian region, which has been identified as a hotspot of plant diversity within the Mediterranean Basin (Médail and Quézel 1997). The singularity and

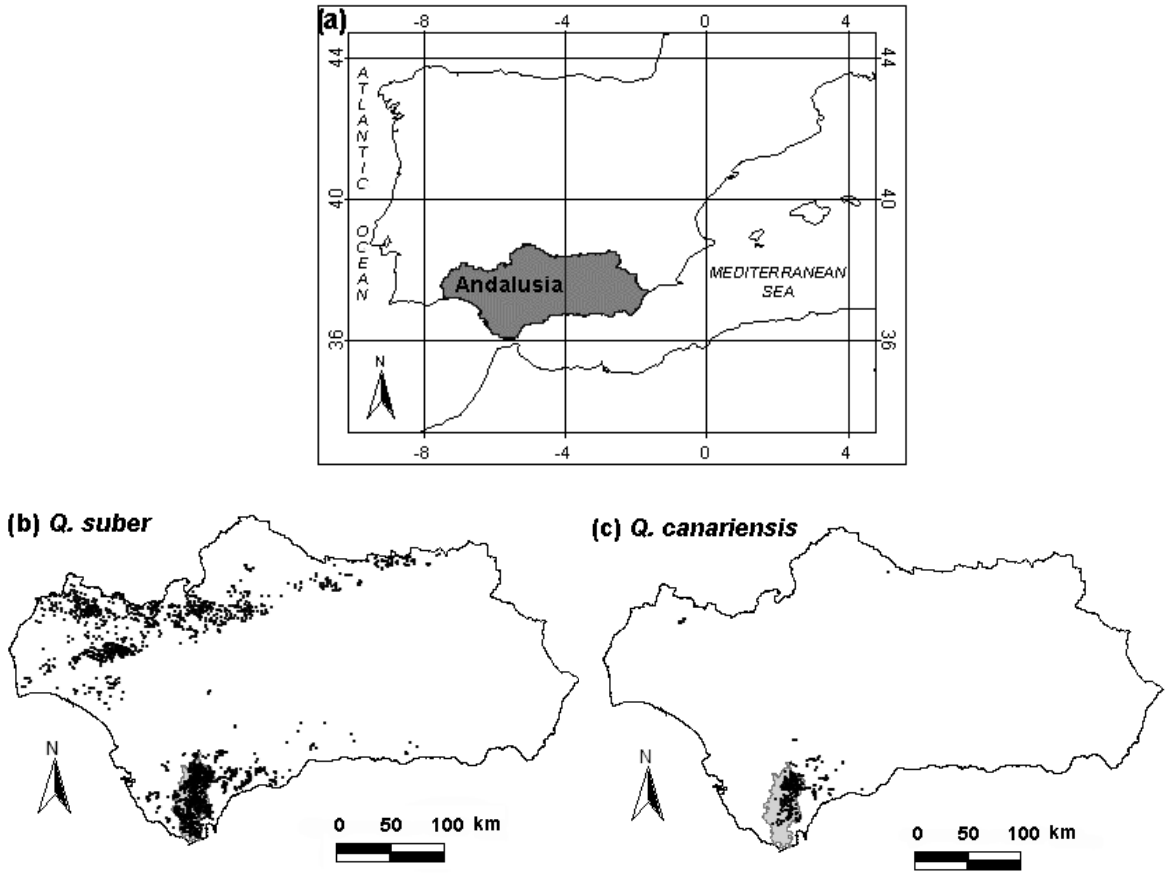

Figure 3.1 Study area in southern Iberian Peninsula (a). Distribution of *Q. suber* (n=1983) (b) and *Q. canariensis* (n=300) (c), based on presence data of the Spanish Second Forest Inventory (SSFI, total of 12572 plots in Andalusia). The grey area in the distribution map (c) corresponds to Los Alcornocales Natural Park's limits (~1700 km^2).

high biodiversity value of this area, as a refuge for some taxa of Tertiary flora, has persisted in terms of both its ecological function and its genetic resources (see Mejías *et al*. 2007; Rodríguez-Sánchez *et al*. in press). The forests occur on acidic, nutrient-poor, sandy soils, derived from Oligo-Miocene sandstone, which harbour a rich endemic flora (Ojeda *et al*. 1996). The topography is mountainous, and maximum elevation is 1092 m a.s.l. The climate is subhumid Mediterranean, with the heaviest rainfall in autumn, winter and spring, but with warm dry summers. Mean annual precipitation ranges from 800 mm near the coast to 1400 mm inland (exceeding 2000 mm in some years), and the mean annual temperature is 15-17 ºC. A combination of ecological factors and favourable historical events may explain the exceptional survival of this wooded mountain landscape within the much deforested Mediterranean region (Marañón and Ojeda 1998).

Historical changes in oak forest composition

We compiled historical data from periodically inventoried public forest estates located in the area of Los Alcornocales Natural Park, in order to analyse changes in *Q. suber* and *Q. canariensis* stand composition during the last one hundred years. In particular, we analysed a sequence of historical management plans drawn up over the past century, which contained quantitative forest inventories and described management practices (see Appendix 3.1 for detailed information on the forest management plans consulted). We focused on nine

public forest estates covering a total area of approximately 40000 ha (see Fig. 3.3 for forest location). The first management plans dated from the end of the nineteenth century, when cork harvesting and manufacture started to intensify in the study area. Subsequently, every 10-15 years, forest inventories were updated and management plans revised. Inventories consisted of the individual counting of all trees with a diameter ≥10 cm in each of the blocks of about 20-30 ha delimited as management areas. Historical inventories did not include measurement of the diameter of individual trees, but rather an estimate of the number of individuals per diametric class (only for *Q. suber* and *Q. canariensis*). Thus, we annotated the total number of *Q. suber* and *Q. canariensis* individuals in each forest, and the rest of the tree species were grouped in a separate category as "other species".

Statistical analysis

We analysed changes in *Q. suber* and *Q. canariensis* density (individuals per total forest area in hectares) over the twentieth century in each of the nine forests targeted. The percentage of individuals per species was calculated at different periods, and changes in forest composition were examined, with emphasis on documented disturbances and forest management practices. We also explored and discussed the possible relationship between the general tendency of forest composition change and socio-economic indicators, such as the evolution of the cork trade from the second half of the nineteenth century onwards. Data were compiled by Parejo (2004), and homogenised to a unified currency and year (pesetas of year 2000), taking into account the fluctuations suffered in the price indexes in each historical period. We expressed the exported and imported values of raw cork (non-manufactured) in euros.

Finally, we explored and discussed the possible relationship between the general trend of forest composition change and the temporal trend in temperature and precipitation in the study area from the beginning of the past century to date, and detected possible anomalies or fluctuations that could have affected the studied species. We analysed time series with moving averages (Štepánek 2006), and calculated regression coefficients with time as independent variable. For this purpose, we selected historical records available from two meteorological stations: Grazalema (900 m a.s.l., series 1912-2000, provided by the Spanish Institute of Meteorology) and Gibraltar (5 m a.s.l, series 1840-2004, provided by GHCN, National Climatic Data Center, USA), located north-east and south of the study area respectively.

Present-day stand structure and environmental gradients

Landscape scale

At a landscape scale, we selected Los Arenales public forest estate, a 284 ha forest area where the two *Quercus* species co-occur, to analyse current forest structure along topographic gradients (see the forest marked with letter "e" in Fig. 3.3 for location). A detailed forest inventory (Egmasa 2003) was available, consisting of a grid of 129 circular (20 m radius) plots, one every 150 metres, defined by their spatial location (UTM coordinates). Sampling consisted of counting all trees and measuring (with a calliper) the trunk diameter at breast height (dbh; with breast height established as 1.3 m) of trees with a dbh >7.4 cm. We computed species basal area per plot, expressed in m^2/ha, as a measurement of species abundance.

Additionally, each inventory plot was characterised with independent topographic data, using a Geographical Information System (GIS) (ArcView 3.2, ESRI Inc., Redlands, USA, 2000). We derived altitude (m), slope (%), and aspect (º) from a 20 m spatial resolution Digital Elevation Model (DEM), obtained from colour aerial photographs (scale 1:60000, provided by REDIAM -the Environmental Information Network of the Andalusian Government). The water flow accumulation map of the area

around the forest was created with HydroTools 1.0 for ArcView 3.2 (Schaüble 2003), using a single-flow algorithm that computes the amount of water moving from water divides to valley floors. Pixels with the highest accumulation values were reclassified as part of the drainage network of the catchment area. We then calculated the distance of each inventory plot from the nearest stream bed. Finally, we constructed a map of access-cost, i.e. the cost or effort of reaching each plot from the main forest tracks/roads, which could be interpreted as an index of the socio-economic value of forest stands and human pressure (for example, as an approximate measurement of the cost of extracting cork in terms of accessibility). We digitised the tracks from maps and orthophotographs, and then used the cost-distance function of ArcView 3.2, including the distance from forest tracks to plots, and the slope map as a friction surface in the algorithm.

Regional scale

At a regional scale, data from the SSFI (Spanish Second Forest Inventory) were analysed in order to study current species distribution and forest composition in Andalusia along climatic gradients (see selected variables below). The SSFI inventory sampled wooded areas of the region in the period 1994-1996, based on a regular grid of survey plots with a density of approximately one circular plot per square kilometre (MMA 1996). Plots were circular, of various concentric radii (the minimum tree diameter measured varied with the radius of the plot), and were defined by their spatial location (UTM coordinates). The dbh of all trees with a dbh >7.4 cm was measured with a calliper. The inclusion of a tree in the sample was a function of its dbh and its distance from the centre of the plot.

Prior to the analyses, we checked the geographic position of all inventoried plots, superimposing them onto wooded areas of recent digital orthophotographs (JA 2003). Plots with georeferencing errors were rejected for the analyses. Subsequently, we extracted a total of 12572 records containing the presence/absence of each species. In plots where *Q. suber* and/or *Q. canariensis* were present, we calculated their basal area, expressed in m^2/ha. Additionally, each inventory plot was characterised with independent environmental data, using a GIS. Climatic data with 1 km spatial resolution were provided by the Spanish Institute of Meteorology as an interpolation (by kriging) of the information recorded from 1971 to 2000 in meteorological stations spread all over the Spanish territory (143 main stations, 1504 thermometric stations, and 4835 pluviometric stations) (INM unpublished).

We selected the following climatic variables: monthly and annual mean precipitation (P) (mm), annual mean radiation (RAD) (kW×h/m^2), and monthly and annual mean temperature (T) in degrees centigrade (ºC). We also derived the average temperature of the warmest month (TWM) (ºC), average temperature of the coldest month (TCM) (ºC), and thermal oscillation (TOSIC) (ºC). Monthly and annual potential evapotranspiration (PET) (mm) were obtained as a function of mean temperature (Thornthwaite 1948). Computing monthly differences between P and PET, we calculated annual water surplus (WS) (mm) as the sum of positive differences between P and PET, annual water deficit (WD) (mm) as the sum of negative P-PET differences, and drought length (DL) as the number of months in which PET exceeded P. Finally, altitude (m) was derived from a DEM of 20 m spatial resolution.

Statistical analysis

We analysed whether present-day oak species abundance, i.e. basal area, was correlated with environmental gradients at landscape and regional scales. Because of the triangular and factor-ceiling distributions (sensu Thomson *et al*. 1996) found in the bivariate vegetation-environment relationships, we calibrated data-specific maximum-likelihood estimators, which are suitable for detecting biological signals within

heteroscedastic patterns (e.g., Floret *et al*. 1990; Zavala 2000). We selected those inventory plots where either one of the species or the sum of the two contributed to at least 95% of the total basal area of the stand. Based on exploratory analyses of potential distributions that best fitted our data, a gamma error distribution of species basal area was assumed, defined by a shape parameter n, which varies from exponential-like to bell-shaped but left-skewed forms. We specified the mean of the gamma distribution as a function of climatic or topographic variables, testing different functional forms that covered a wide range of possible responses: linear, exponential, power, and Michaelis-Menten-type.

All statistical models were parameterised with maximum likelihood (Edwards 1992), using a simulating annealing algorithm (Metropolis *et al*. 1953). Parameter 95% support limits were estimated by likelihood profile (Hilborn and Mangel 1997). In order to determine which variables were most strongly associated with species abundance, fitted models were compared with a null model of no factor effect through a Likelihood Ratio Test (LRT) (0.05 level), in which the degrees of freedom were equal to the difference in the number of parameters between models (Edwards 1992). Additionally, models were compared using Akaike's Information Criteria, specifically ΔAIC, which is defined for each $Model_i$ as AIC_i - AIC minimum (Akaike 1992). Models with ΔAIC of 0-2 were considered to have equivalent and substantial empirical support, ΔAIC of 4-7 indicated less support, and models with ΔAIC >10 had very low empirical support (Burnham and Anderson 2002). All models and numerical algorithms were implemented in C (Borland C++ v.5.01, Borland International Inc., USA, 1996). Finally, we calculated Moran's I autocorrelation coefficient across distance classes for the raw species abundance data, and generated correlograms of model residuals using GS+ 5.1.1. (Gamma Design Software, Michigan, USA, 2001).

Results

Changes in mixed oak forest composition over the last century

A sharp increase in the number of cork oaks was observed in all studied forests (Fig. 3.2a-i), just after the first management plans started at the beginning of the twentieth century (with the exception of one forest, Fig. 3.2a). This trend slowed during the years following the Spanish civil war (1936-1939). Around the decade of the 1960s, there was another general increase in *Q. suber* density. In comparison, the density of *Q. canariensis* was higher than or very similar to that of *Q. suber* in some forests just before management plans started (Fig. 3.2a, b, d, and to a lesser extent, 3.2c). It remained constant, or even increased a little in some areas, during the first decades, but after 1940-50 generally decreased, due to selective logging of *Q. canariensis*, as documented. Species other than *Q. suber* and *Q. canariensis* (such as *Fraxinus angustifolia* Vahl., *Arbutus unedo* L., *Olea europaea* L. var. *sylvestris* Brot., *Pyrus bourgeana* Decne, and *Alnus glutinosa* (L.) Gaertn.) represented a small proportion of forest composition. The density of "other species" increased in some forests, primarily due to pine (*Pinus pinea* L., *P. halepensis* Mill., and *P. pinaster* Ait.) afforestation carried out from the middle of the century onwards (Fig. 3.2).

Overall, there was a shift to dominance by the sclerophyllous *Q. suber* in the study area in a few decades. Its relative density increased in all studied forests, as seen when forest composition at the beginning of the twentieth century was compared with that at the end of the century (Fig. 3.3). This trend was especially noticeable in the forest estates located in areas with higher annual mean precipitation (north of Los Alcornocales Park), where the proportion of deciduous species was greater than that of cork oak at the beginning of the century. Species other than *Quercus* showed an increased proportion in 1970-1980 as a result of pine afforestations.

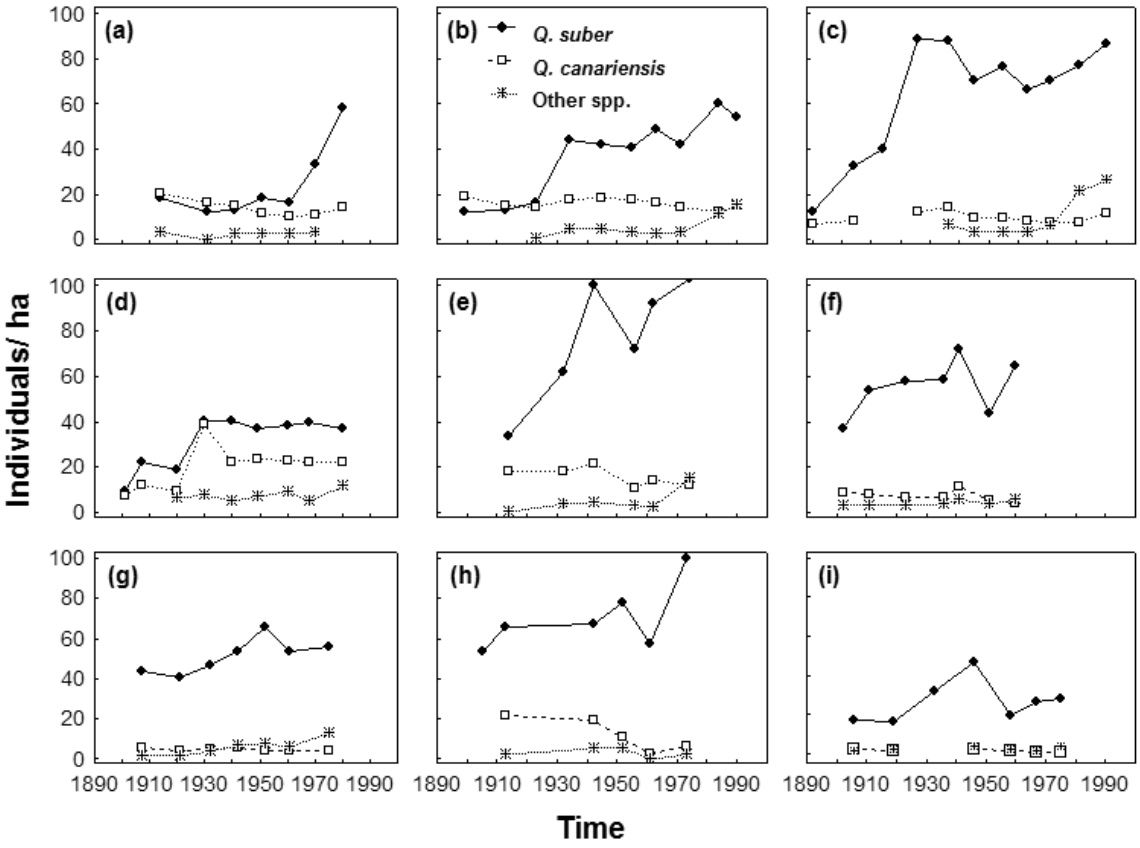

Figure 3.2 Changes in the number of individuals per hectare for *Q. suber*, *Q. canariensis*, and "other species", over the last century in each of the surveyed public forest estates (a-i). Other species inventoried included *Fraxinus angustifolia* Vahl., *Arbutus unedo* L., *Olea europaea* L. var. *sylvestris* Brot., *Pyrus bourgeana* Decne, *Alnus glutinosa* (L.) Gaertn, *Quercus ilex* L. (only in "a" and "d"), *Eucalyptus camaldulensis* Dehnh., and pines (*Pinus pinea* L., *P. halepensis* Mill., or *P. pinaster* Ait.) which were introduced from 1960 on. Note that species density (nº individuals) has been related to the total surface (ha) of each forest estate (including non-forested areas) for comparison among different inventories over time. See Fig. 3.3 for the geographic location of the forests (indicated with the same letters), and Appendix 3.1 for data sources.

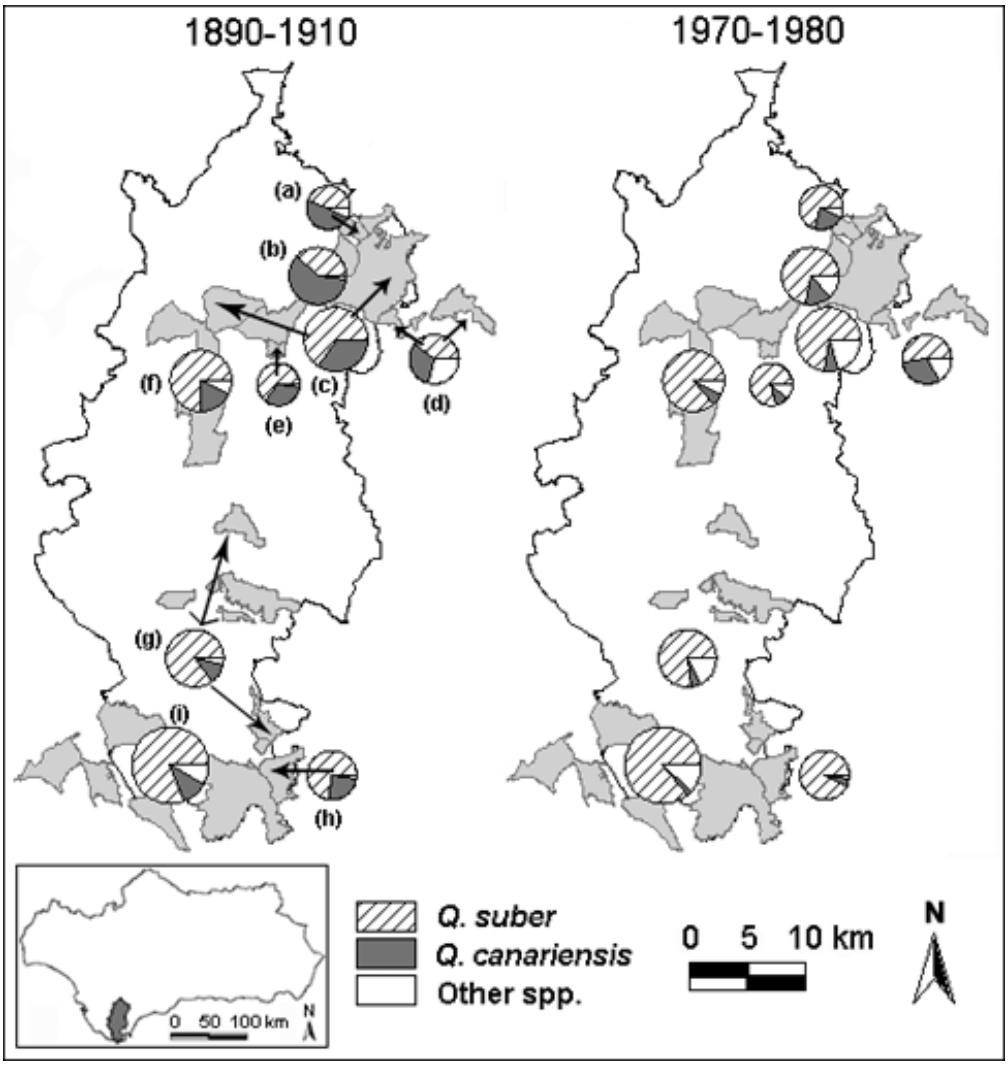

Figure 3.3 Changes in mixed *Q. suber- Q. canariensis* forest composition over the twentieth century in the area of Los Alcornocales Natural Park (limits in black line). Species percentage in each of the inventoried public forest estates (grey areas) at the beginning of the century (1890-1910) are compared to species relative abundance in the last shared historical inventories (1970-80). Charts are drawn on top of the corresponding forest and are proportional to the forest surface. Arrows indicate separated management areas of the same forest estate. An increase in cork oak proportion is observed at the expense of *Q. canariensis*, especially in northern areas with higher precipitation regimes.

Averaged over the nine forest estates, the number of cork oaks per hectare increased sharply through the twentieth century, especially during the first decades and the last quarter of the twentieth century, whereas *Q. canariensis* showed oscillations in its mean abundance (Fig. 3.4a). Over the same period, the Spanish export trade of cork generally increased (Fig. 3.4b), although it fluctuated. Decreases in the trade were linked to the periods of the two world wars and more significantly to the Spanish civil war, after which the commercial leadership significantly decreased, until the recent recovery. The abundance of imported cork was very low, even zero, up until to the last few decades when it has since become a major crop plant (Fig. 3.4b).

Historical records of meteorological stations showed a gradient of decreasing rainfall from north (inland mountains) to south (coast) of the study area, with fluctuations between years. Mean yearly rainfall in the north (Grazalema, series 1912-2000) was 2097 mm ± 774 mm standard deviation (SD) (range from 584 mm to 4000 mm in some years) (Fig. 3.4c). Whereas mean rainfall recorded in Gibraltar (series 1840-2004) was 822 mm ± 270 mm SD in the south,

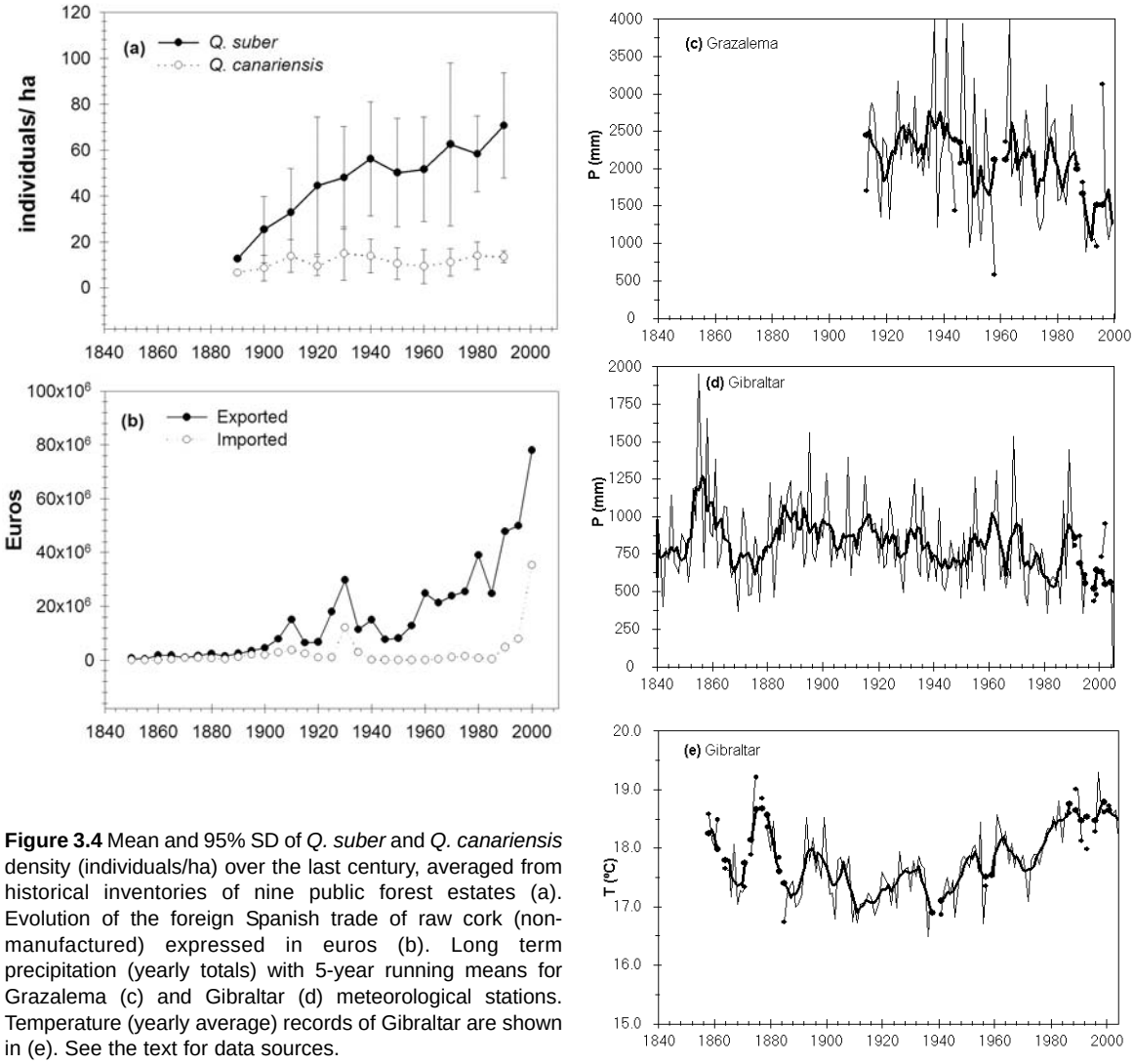

Figure 3.4 Mean and 95% SD of *Q. suber* and *Q. canariensis* density (individuals/ha) over the last century, averaged from historical inventories of nine public forest estates (a). Evolution of the foreign Spanish trade of raw cork (non-manufactured) expressed in euros (b). Long term precipitation (yearly totals) with 5-year running means for Grazalema (c) and Gibraltar (d) meteorological stations. Temperature (yearly average) records of Gibraltar are shown in (e). See the text for data sources.

reaching maximum values of 1955 mm and minimum of 356 mm (Fig. 3.4d). The regression model between mean rainfall and time had a significant negative slope, revealing a trend of a decrease in annual mean precipitation (with a trend/10years of -97.07 mm in the north and -12.62 mm in the south). Nonetheless, both climatic records showed runs of years well above or below the long-term mean, with alternate dry and wet periods. Temperature records showed fluctuations but without abrupt changes; nevertheless, as a general trend, mean temperature has progressively increased (trend/10 years of 0.05 ºC) in the study area since the beginning of the twentieth century (Fig. 3.4e).

Landscape scale: patterns along topographic gradients

The local forest inventory revealed that Los Arenales forest estate is today mainly composed of *Q. suber* (found in 80% of the plots) and *Q. canariensis* (found in 52% of the plots). *Q. suber* occupies a high percentage of the stand basal area, and is found mixed with *Q. canariensis* in 59 out of 129 inventory plots. This pattern is in accord with the trend observed in the historical time series analysed for this forest, where *Q. suber* had dramatically increased (see "e" in Figs. 3.2 and 3.3). Other tree species, such as *A. unedo*, *O. europaea* var. sylv., *P. bourgeana*, and *A. glutinosa* are present but less abundant. Eucalyptus and pines have been planted at sites where oak forests were absent.

Parameter estimates that gave best fits relating species basal area with topographic factors are summarised in Table 3.1. As indicated by best-supported models (ΔAIC=0; LRT, p<0.001), the distance from a watercourse best explained the two species' abundance in the landscape (Fig. 3.5a), although with contrasting direction (positive slope (p_2) for *Q. suber*, and negative for *Q. canariensis*, Table 3.1). That is, while mean basal area of *Q.* suber increased exponentially with distance from a watercourse, the opposite relationship was found for *Q. canariensis*, which was more abundant near stream beds (Fig. 3.5b). The model including drainage reduced spatial autocorrelation at short distances (150 m) for *Q. canariensis*, but did not account for the spatial pattern in *Q. suber* abundance (Appendix 3.2a, b). The altitude gave fits of

Table 3.1 Maximum likelihood parameter estimates for best-fit models relating *Q. suber* (n=94) and *Q. canariensis* (n=53) basal area (m^2/ha) to topographic factors.

	Factor	Best fit	n	p_1	p_2	LogLike.	LRT (X^2)	p	AIC	ΔAIC
Q. suber	Distance from drainage	EXP	1.4	7.1	0.0049	-305.1	14.6	***	616.2	0.0
	Access-cost	EXP	1.5	6.9	0.0001	-305.2	14.4	***	616.4	0.2
	Altitude	LIN	1.5	-2.4	0.0528	-305.3	14.3	***	616.5	0.3
	Factor	**Best fit**	**n**	**p_1**	**p_2**	**LogLike.**	**LRT (X^2)**	**p**	**AIC**	**ΔAIC**
Q. can	Distance from drainage	EXP	1.0	10.6	-0.0106	-148.8	12.1	***	303.6	0.0
	Access-cost	EXP	0.9	8.9	-0.0001	-152.5	4.7	*	311.0	7.4

Note: Best fits were found for the Exponential (EXP) response, where species' mean basal area= $p_1 e^{(p_2 Factor_i)}$; p_1 and p_2 are maximum likelihood parameter estimates, n is the shape parameter estimated for the gamma distribution of basal areas, where n ~1.5 indicates bell-shaped but left-skewed probability distribution, and n <1 exponential-like monotonically decreasing distribution.

LogLike. corresponds to the maximum log-likelihood: log(Lq|data, model). AIC (Akaike's Information Criteria) is calculated as: AIC = -2log(Lq|data, model) + 2K, being K the number of parameters in the model. Factors' effects are evaluated through the loglikelihood ratio test (LRT, df=1, *p<0.05, **p<0.01, ***p<0.001), and model fits through ΔAIC (AIC_i- AIC_{min}).

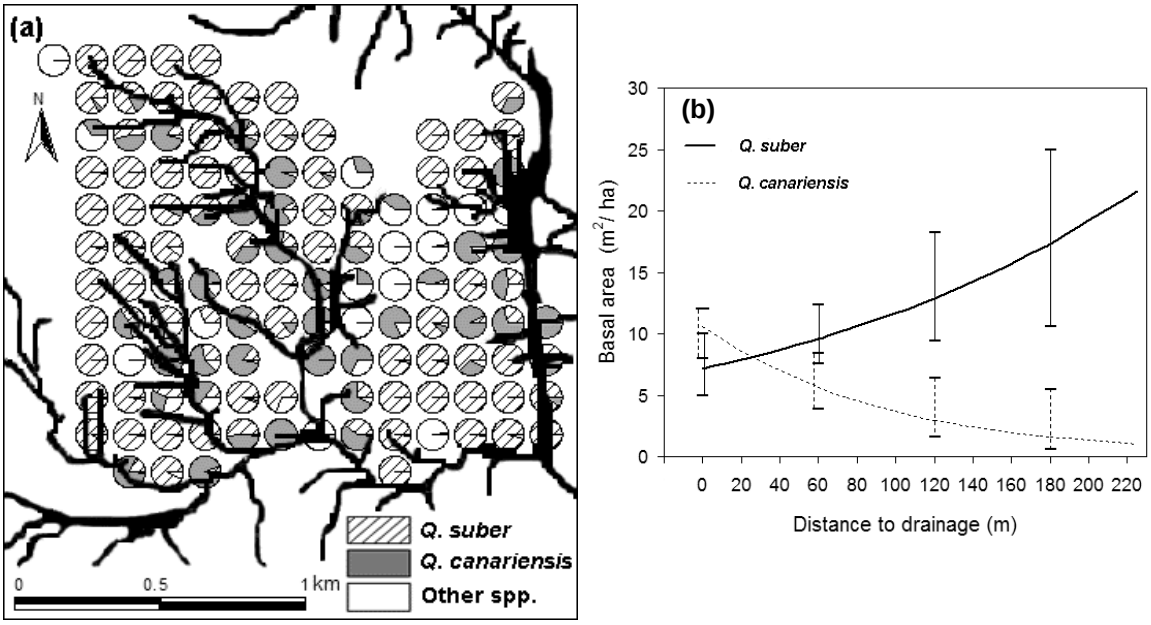

Figure 3.5 *Q. suber* and *Q. canariensis* distribution at landscape scale, in Los Arenales forest estate, along the drainage network (black line). See "e" in Fig. 3.3 for forest location. Sectors within charts are proportional to the percentage of species basal area in each inventory plot. "Other species" include mainly pines (*Pinus pinea*, *P. halepensis*, and *P. pinaster*), and to a lesser extent *Arbutus unedo*, *Olea europaea* var. *sylvestris*, *Pyrus bourgeana* and *Alnus glutinosa* (a). Differential response of *Quercus* species mean basal area (with 95% confidence intervals) along the gradient of distance to the drainage network, based on best model fits of local inventory data (b).

similar empirical support (ΔAIC<2) for *Q. suber*, with a positive relationship (i.e., its abundance increased with the altitude), but had negligible influence on *Q. canariensis* (Table 3.1). The variable quantifying the cost of reaching each inventory plot from the main forest tracks also had substantial support (within two AIC units of the best supported model) for *Q. suber*, but low support for *Q. canariensis*. Mean basal area of *Q. suber* increased along the access-cost gradient -i.e., its abundance was greatest in areas with low accessibility. Finally, models including altitude and cost reduced the level of spatial autocorrelation at the first distance class for *Q. suber* (Appendix 3.2a).

Regional scale: patterns along climatic gradients

Parameter estimates of models with the strongest empirical support relating present-day species mean basal area (m^2/ha) with climatic factors at a regional scale are summarised in Table 3.2. The average temperature for the warmest month (TWM) was the best predictor (ΔAIC=0) of *Q. suber* abundance. As temperature increased, mean abundance decreased, following an approximately linear response. Other factors associated with water (i.e., annual precipitation, water surplus, water deficit) and energy (i.e., temperature oscillation) gave a significant fit (LRT, $p<0.001$), but represented models with low empirical support based on ΔAICs. Mean *Q. suber* abundance increased approximately linearly with annual mean precipitation (P) and water surplus (WS), while there was a negative effect of annual water deficit (WD) and temperature oscillation (TOSCI) (with negligible empirical support). For *Q. canariensis*, annual mean precipitation best explained its abundance (LRT, $p<0.05$), following a positive and approximately linear relationship (Table 3.2). With similar empirical support (ΔAIC<2), basal area of the deciduous species increased with water surplus and mean radiation, whereas it decreased with water deficit.

Table 3.2 Maximum likelihood parameter estimates for best-fit models relating *Q. suber* (n=1983) and *Q. canariensis* (n=300) basal area (m^2/ha) to climatic factors at the regional scale.

	Factor	n	p_1	p_2	LogLike.	LRT (X^2)	p	AIC	ΔAIC
Q. suber	T Warmest Month (TWM)	1.6	80.6	-2.8680	-2280.1	116.3	***	4566.1	0.0
	Annual P	1.6	-4.5	0.0155	-2286.6	103.2	***	4579.2	13.1
	Annual Water Surplus (WS)	1.6	0.5	0.0168	-2287.0	102.5	***	4580.0	13.9
	Annual Water Deficit (WD)	1.5	33.6	-0.0519	-2296.7	83.0	***	4599.4	33.3
	T Oscillation (TOSCI)	1.5	28.0	-1.2230	-2304.2	68.1	***	4614.4	48.3
	Factor	**n**	**p_1**	**p_2**	**LogLike.**	**LRT (X^2)**	**p**	**AIC**	**ΔAIC**
Q. can	Annual P	1.3	-12.5	0.0182	-355.0	8.1	**	716.1	0.0
	Annual Water Surplus (WS)	1.2	-5.8	0.0182	-355.6	7.0	**	717.2	1.1
	Annual Radiation (RAD)	1.2	-95.8	23.8900	-355.9	6.3	*	717.9	1.8
	Annual Water Deficit (WD)	1.2	31.6	-0.0570	-356.1	6.0	*	718.2	2.1

Note: Best fits were found for the linear response, where species' mean basal area= $p_1 + p_2 Factor_i$; p_1 and p_2 are maximum likelihood parameter estimates, n is the shape parameter estimated for the gamma distribution of basal areas, where n ~1.5 indicates bell-shaped but left-skewed probability distribution. Models are evaluated as in Table 3.1, through loglikelihood ratio tests (LRT, df=1, *p<0.05, **p<0.01, ***p<0.001), and ΔAIC ($AIC_i - AIC_{min}$).

To study interspecific differences, the abundance of each species was analysed along the annual mean precipitation gradient -i.e., the best predictor for *Q. canariensis* and the second best for *Q. suber*. Models had similar positive slopes, but species differed in the intercept parameter (p_1) (Table 3.2). *Q. suber* was present from 500 mm precipitation onwards, whereas the lower limit for *Q. canariensis* was 800 mm (Fig. 3.6a). The two species co-occurred at the wetter end of the gradient (800 mm onwards), where stand structure showed a greater variance. Examination of residuals indicated that models accounted for most of the spatial pattern in species abundance, except for *Q. suber* at short distances (Appendix 3.2c, d).

Discussion

Studying mixed oak forests by means of multiscale focus (both temporal and spatial) enabled us to identify key environmental factors influencing forest composition, as well as historical processes underlying present-day patterns. Results quantitatively highlight surprisingly rapid changes in forest composition over the past century in a Mediterranean landscape, reinforcing the evidence of human activities as the main drivers of recent forest dynamics.

Drivers of change in mixed oak forest composition in the last century

The analyses of historical forest inventory data revealed an increasing dominance of *Q. suber* during the twentieth century in all studied mixed forests, whereas *Q. canariensis* remained constant or even decreased in some periods. *Q. suber* expanded, and the number of individuals increased sharply, in a few decades in the most-productive areas (with higher annual precipitation, see Fig. 3.3), where *Q. canariensis* would find most-favourable conditions.

The first forest management plans, from the end of the nineteenth century, considered *Q. canariensis* a principal forest species together with *Q. suber*, particularly in those sites where the two species co-dominated (González *et al*. 1996). *Q. canariensis* wood was pollarded for charcoal production, and was used in railway construction (Jurado 2002). However, due to the increasing demand for cork as bottle stoppers, forest management restored plant cover by favouring the economically most valuable species, *Q. suber*, through seedling plantations and acorn sowing, and taking advantage of its extraordinary resprouting capacity from stem and basal buds. The traditional use of cork oak bark in leather tanning was progressively abandoned, and forests were divided into regular stands with trees of the same age in order to facilitate bark stripping approximately every decade. Conversely, *Q. canariensis* trees suffered selective clear-cuttings, as documented in some of the inventories, especially when alternative sources of energy (e.g., butane gas) replaced charcoal in the 1950-60s. Nevertheless, *Q. canariensis* stands were not completely substituted by cork oaks, given the complementary resources they provided, such as earlier seed production, which lengthened the period of acorn availability and improved animal feeding in mixed stands, and its nutrient-richer litter, which was believed to increase soil fertility and moisture.

On one hand, forest composition changes reported could be partly attributable to recent fluctuations in climate. A general decline in rainfall and a warming of up to 1 ºC, most marked in winter, have been observed over the twentieth century in the study area (Wheeler and Martín-Vide 1992), but the magnitude of wet/dry year fluctuations seems similar in the past and present (Rodrigo *et al*. 2000). Inter-annual variations in climatic conditions most probably have had a differential influence on short-term processes such as fecundity, seedling survival, or tree growth (e.g., Costa *et al*. 2002), but were not intense enough (for example as episodic droughts) to result in a significant adult tree mortality. Therefore, it is questionable whether the observed sharp changes in forest composition can be attributed to fluctuations in precipitation and temperature, given the long-term response of forests to those factors.

On the other hand, the impact of human activities may have modified the distribution of species outside the potential limit established by the environment (Thomson *et al*. 1996). This could be more likely for tree species such as oaks, which historically have been managed by human populations (Foster *et al*. 2002; Johnson *et al*. 2002). *Q. suber* has been artificially favoured and conserved in many parts of its natural range (Montoya 1988; Vieira Natividade 1991). Consequently, we support the inference that forest composition changes reported in the present study, which are reflected in present-day forest structure, are probably human-induced, due to their rate and magnitude.

Likewise, in holm oak (*Q. ilex*) stands (dehesas) of central and north-east Spain, land-use history and management have been found to be the most important factors determining current forest composition and structure (Gracia and Retana 1996; Joffre *et al*. 1999; Pulido *et al*. 2001; Plieninger *et al*. 2003). Other examples of the positive impact of human activities on certain tree species are, for example, olive tree (*Olea europaea* L.) domestication in the Mediterranean Basin (e.g., Terral *et al*. 2004), anthropogenic savannas with *Acacia caven* Mol. (espinales) in central Chile (e.g., Ovalle *et al*. 1996), increased dominance of *Acer rubrum* L. (red maple), *Betula* spp. (birch), and oak species following disturbances caused by post-settlement human activities in eastern North America (e.g., Abrams 1998; Bürgi *et al*. 2000), and *Pinus* and *Eucalyptus* genera widely planted outside their natural ranges in many zones for commercial forestry (e.g., Zobel *et al*. 1987; Richardson *et al*. 1994).

Influence of environmental factors on present-day mixed oak forest structure

Today, and partly as a consequence of reported historical changes in forest composition, the evergreen *Q. suber* is more abundant in a wider range of environmental conditions than is the deciduous *Q. canariensis*, which is restricted to areas with a high precipitation regime, lower water deficit, mild temperatures, and frequent mist in the mountains near the Strait of Gibraltar. Mean abundance of *Q. suber* and *Q. canariensis* increases with annual precipitation, and the two co-occur above 800 mm. However, accurate prediction of species basal area for a given point of the precipitation gradient is difficult, due to the effect of site factors, such as topographic variation and stand management history, which have influenced forest structure locally.

By reducing the scale of analysis to that of the landscape (Los Arenales forest, 1100 mm mean rainfall), where regional models would predict the co-occurrence of *Q. suber* and *Q. canariensis*, we observed that oak species were not randomly distributed in the landscape, but instead segregated along a gradient of water availability (i.e., distance from stream beds). The deciduous species, *Q. canariensis*, was found clearly associated with areas near streams, where microclimatic conditions (warm and moist) are in marked contrast with drier adjacent habitats, where *Q. suber* is more abundant, suggesting that *Q. canariensis* performs better than *Q. suber* under moister conditions. In Mediterranean ecosystems, factors associated with water availability are commonly found to have great influence on forest composition (Pigott and Pigott 1993; Zavala *et al*. 2000). Oak species' differential distribution patterns found along the water availability gradient might be partly determined by species' contrasting physiological and morphological features (Marañón *et al*. 2004; Quero *et al*. 2006). Under controlled greenhouse conditions, water treatments modified physiological traits of deciduous species (*Q. canariensis* and *Q. pyrenaica*), increasing their stomatal conductance, photosynthesis, and respiration rate, but had little effect on *Q. suber* seedlings (Quero *et al*. 2006). Furthermore, in a field experiment, water addition during the dry period (simulating sporadic rains) reduced mortality of *Q. canariensis* seedlings, whereas *Q. suber* was not affected (see chapter 5).

On the basis of our results, we suggest that in the absence of human intervention, cork oak and *Q. canariensis* would have been more clearly segregated, with deciduous oaks dominating in the more humid areas (see Fig. 3.6b). Cork oak is currently a valuable species from the point of view of forest ecosystem conservation, and still has strong socio-economic implications for the cork industry. As revealed by the accessibility-cost analysis, *Q. suber* dominates in less accessible stands, despite the greater cost of reaching them, indicating that cork extraction and transport by mules has been a common practice in the whole forest area. Although the cork industry has suffered fluctuations over the century, with severe competition in recent years from synthetics (see Parsons 1962; Parejo 2004), the cork currently harvested in the area of Los Alcornocales Park represents approximately 30% of the Spanish and 8% of the world production (Anonymous 2004).

Future trends in forest composition and dynamics remain somewhat uncertain. A general decline and impaired regeneration has been detected in cork oak stands on both sides of the Strait of Gibraltar (Ajbilou *et al*. 2006), coupled with a reduction in cork production (Linares and Fariña 2002). Current management plans are implemented to reduce oak seedling mortality by large-scale fencing and exclusion of herbivores, as well as reforestations of *Q. suber* and other species. The Algerian oak (*Q. canariensis*), despite the historical reduction of its distribution area to favour cork oak, is expected to show an upward trend locally. *Q. canariensis* stands are currently protected as forest habitat (considered trees "of special interest" by regional laws), due to their rich understorey with high

taxonomic singularity (Ojeda *et al*. 1996). It would thus be reasonable to predict a trend of continuous replacement of old, injured (by periodic bark removal) cork oaks by young, vigorous deciduous oaks in those wetter and more-fertile areas where management has modified forest composition. At a longer time scale, both oak species will be severely affected by the climate change prediction of warmer and drier conditions for this Mediterranean region (Schröter *et al*. 2005).

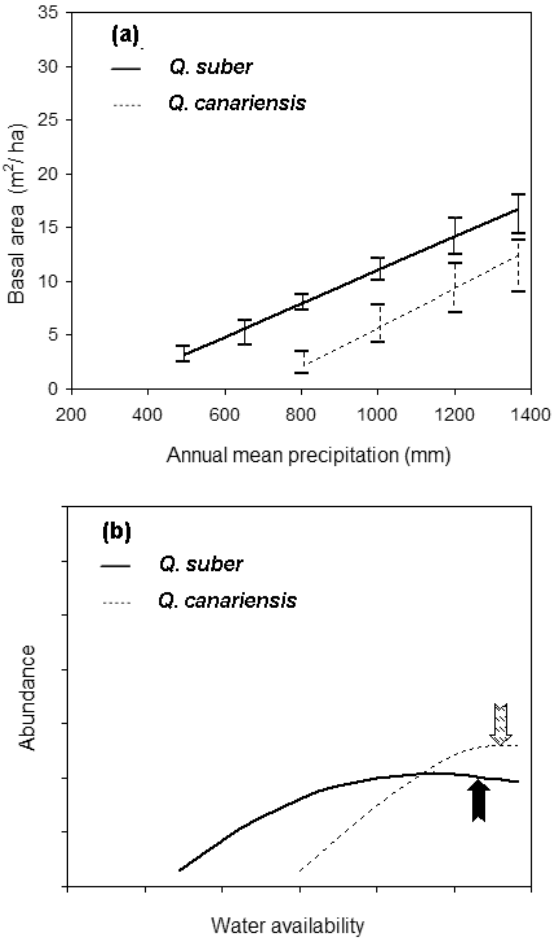

Figure 3.6 Species mean basal area (with 95% confidence intervals) along the gradient of annual mean precipitation (P), based on best model fits of SSFI data. Both species abundance (basal area) increases along the P gradient, and they co-occur 800 mm onwards (the lowest limit of *Q. canariensis*) (a). Representation of potential (without human intervention) distribution niches of evergreen and deciduous *Quercus* species, along a gradient of water availability (b). Arrows indicate the direction of human influence on each species. We suggest that in rainy areas humans have favoured *Q. suber* and reduced *Q. canariensis*' area. Panel (b) has been drawn to be compared to the current patterns observed in (a).

In conclusion, our study quantitatively exemplifies a human-mediated shift in forest composition. As a result of forest management, the realized niche of the cork oak has been enlarged at the expense of that of *Q. canariensis*, providing further evidence of humans as main drivers of oak forest composition and structure across the Mediterranean region. The present study supports palynological data which suggest that, in the absence of human influence, *Q. suber* would develop in mixed forests, sharing the arboreal stratum with other sclerophyllous species and with deciduous ones (Reille 1977; Carrión *et al*. 2000). Recent regeneration problems detected in *Q. suber* stands, a lesser demand for wood products, conservation policies, and climate change augur new large-scale shifts in forest composition.

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Appendix 3.1

References of the management plans and forest inventories consulted for the analysis of historical changes in mixed oak forest composition (area of Los Alcornocales Natural Park, S Spain). Letters next to the name of the public forest estates correspond to their geographic position in the maps of Figure 3.3.

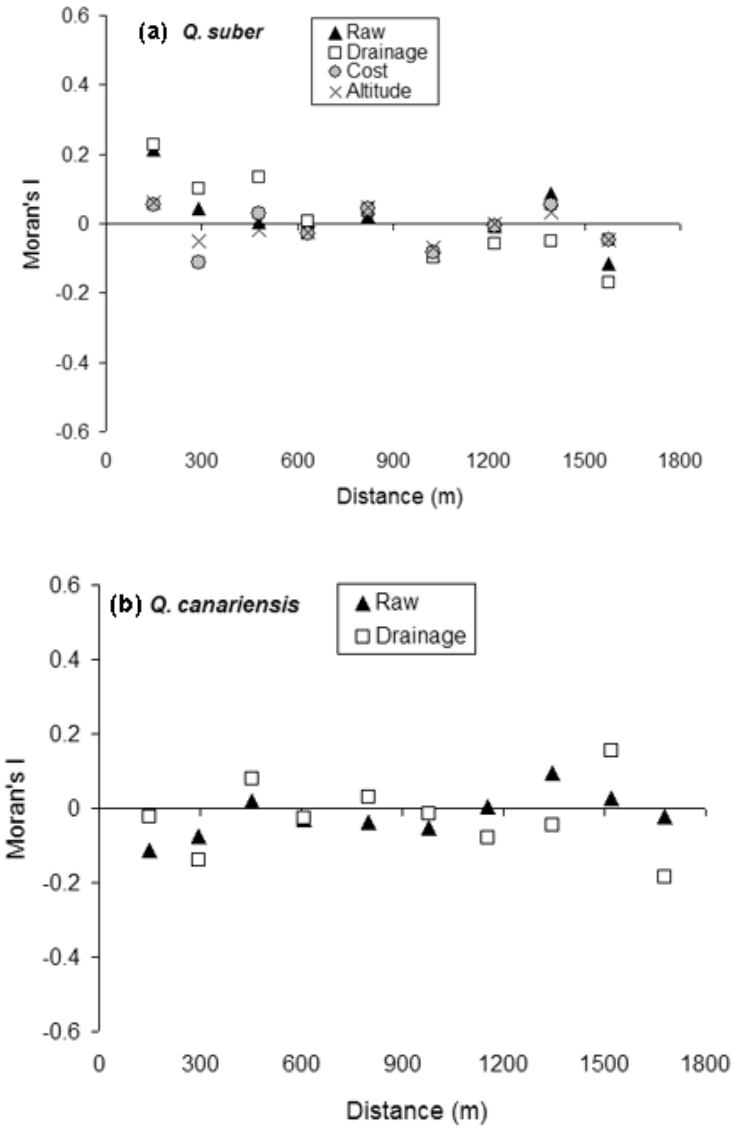
Forest	Surface (ha)	Author	Year	Forest Management Plan
La Cancha (a)	468	García, J.	1914	Proyecto de ordenación del monte "La Cancha". Propio de Villaluenga del Rosario.
		García, A.	1931	Proyecto de revisión ordinaria y segundo plan especial de aprovechamientos y mejoras correspondiente al monte "La Cancha".
		García, A.	1941	Proyecto de segunda revisión ordinaria y tercer plan especial de aprovechamientos y mejoras correspondiente al monte "La Cancha", nº 31 del catálogo y de la pertenencia de los Propios de Villaluenga del Rosario.
		García, L.	1951	Proyecto de tercera revisión ordinaria y cuarto plan especial de aprovechamientos y mejoras del monte "La Cancha", nº 31 del catálogo.
		García, L.	1961	Proyecto de cuarta revisión ordinaria y quinto plan especial de aprovechamientos y mejoras del monte "La Cancha", nº 31 del catálogo.
		Sánchez, P.	1970	Proyecto de quinta revisión ordinaria y sexto plan especial de aprovechamientos y mejoras del monte "La Cancha", nº 31 del catálogo.
		Lozano, A.	1980	Proyecto de sexta revisión ordinaria y séptimo plan de aprovechamientos y mejoras del monte "La Cancha" de Villaluenga del Rosario, nº 31 del catálogo. Término municipal de Cortes de la Frontera.
Las Majadas de Ronda (b)	4102			from González, A., Torres, E., Montero, G. & Vázquez, J. (1996) Resultados de cien años de aplicación de la selvicultura y la ordenación de montes alcornocales de Cortes de la Frontera (Málaga), 1890-1990. Revista Montes 43: 12-22.
Grupo Cortes de la Frontera (c)	6895			from González, A., Torres, E., Montero, G. & Vázquez, J. (1996) Resultados de cien años de aplicación de la selvicultura y la ordenación de montes alcornocales de Cortes de la Frontera (Málaga), 1890-1990. Revista Montes 43: 12-22.

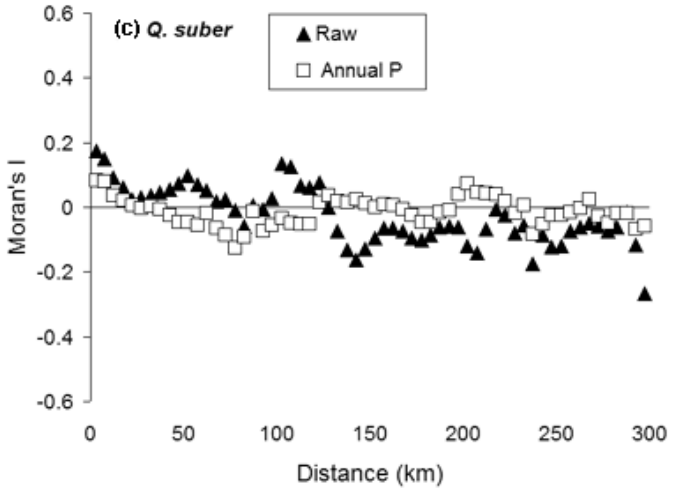
Grupo Gaucín y Algatocín (d)	1661	García, J.	1901	Plan de ordenación y plan de aprovechamientos y mejoras de los montes de Gaucín y Algatocín.
		Illegible	1907	Revisión del proyecto de ordenación del monte "Gaucín y Algatocín". Inventario, ordenación y planos.
		Illegible	1920	Proyecto de revisión ordinaria y tercer plan especial de aprovechamientos y mejoras, correspondientes al grupo denominado "Montes de Gaucín y Algatocín".
		Peña, A.	1930	Proyecto de revisión ordinaria y cuarto plan especial de aprovechamientos y mejoras, correspondientes al grupo denominado "Montes de Gaucín y Algatocín". nº 29 y 36 del catálogo.
		García, A.	1940	Proyecto de 4ª revisión y 5º plan especial de los "Montes de Gaucín".
		García, A.	1949	Proyecto de 5ª revisión y 6º plan especial de los "Montes de Gaucín".
		García, L.	1960	Proyecto de 6ª revisión ordinaria y 7º plan de aprovechamientos y mejoras del grupo de montes "Montes de Gaucín", nº 29 y 36 del catálogo. Términos municipales de Benarraba y Gaucín.
		Sánchez, P.	1968	Proyecto de séptima revisión ordinaria y octavo plan de aprovechamientos y mejoras del grupo de montes "Montes de Gaucín", nº 29 y 36 del catálogo. Términos municipales de Benarraba y Gaucín.
		Lozano, A.	1980	Proyecto de octava revisión y noveno plan especial de aprovechamientos y mejoras del grupo de montes "Montes de Gaucín", de Gaucín y Algatocín, nº 29 y 36 del catálogo de U.P. (Término municipal de Benarraba y Gaucín).
Los Arenales (e)	284	García, J.	1914	Proyecto de ordenación del Monte "Arenales" de Propios de Jimena de la Frontera (Cádiz).
		Avila, G.	1932	Revisión y proyecto del segundo plan especial del Monte "Los Arenales" de Jimena de la Frontera.
		Castro, M.	1942	Segunda revisión del proyecto del tercer plan especial del Monte "Los Arenales" de Jimena de la Frontera.
		Martín, E.	1956	Tercera revisión y cuarto plan especial, decenio 1951-52 al 1960-61, de proyecto de ordenación del monte "Los Arenales", nº 50 de Jimena de la Frontera.
		Robert, F.	1962	Cuarta revisión del proyecto de ordenación del Monte "Los Arenales", nº 50 del catálogo de U.P. y quinto plan especial (decenio 1961-62 al 1970-71). Memoria-Ordenación-Plan Especial.
		García, V.	1974	Quinta revisión del proyecto de ordenación del Monte "Los Arenales", nº 50 del catálogo de U.P. y sexto plan especial (decenio 1971-72 al 1980-81).
Grupo de Alcalá de los Gazules (f)	5899	Olazabal, S.	1902	Proyecto de ordenación de los Montes de "Alcalá de los Gazules". Apeo de rodales.
		Anonymous	1911	Montes de Alcalá de los Gazules. Proyecto de revisión. 2º plan especial de aprovechamientos.
		Quero, L.	1923	Revisión y proyecto del 3º plan especial en los montes de Alcalá de los Gazules de la provincia de Cádiz.
		Castro, M.	1941	Cuarta revisión del proyecto de ordenación de los montes de Alcalá de los Gazules y 5º plan especial. Texto.

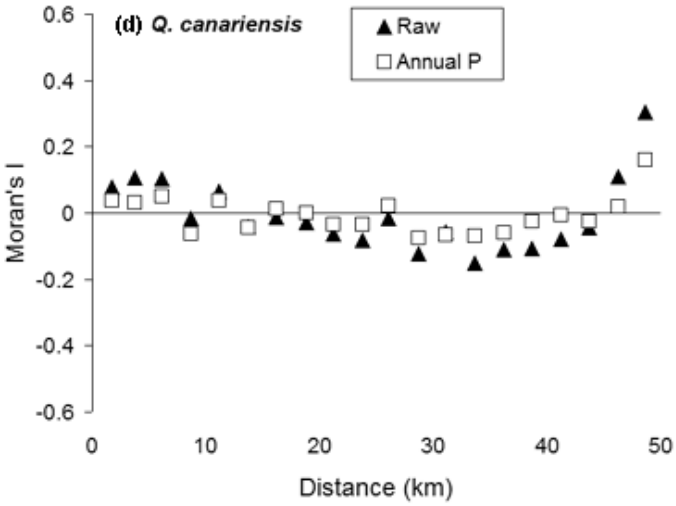
		Castro, M.	1941	Cuarta revisión del proyecto de ordenación de los montes de Alcalá de los Gazules y 5º plan especial. Texto.
		Castro, M.	1951	Quinta revisión del proyecto de ordenación de los montes de Alcalá de los Gazules y sexto plan especial. Memoria.
		Robert, F.	1960	Sexta revisión del proyecto de ordenación del grupo de montes de Alcalá de los Gazules y séptimo plan especial (decenio 1961-62 a 1970-71). Memoria-ordenación-plan especial.
Grupo de Los Barrios (g)	4319	García, J.	1907	Proyecto de ordenación de los montes de propios de "Los Barrios" (Cádiz).
		Quero, L.	1921	Revisión y proyecto de 2º plan especial en los montes de "Los Barrios" de la provincia de Cádiz.
		Avila, G.	1932	Revisión y proyecto de tercer plan especial en los montes de "Los Barrios" de la provincia de Cádiz.
		(Illegible), M.	1942	Cuarta revisión del proyecto de ordenación de los montes de "Los Barrios".
		Castro, M.	1952	Cuarta revisión y quinto plan especial del proyecto de ordenación del Grupo montes de "Los Barrios".
		Gallego, L.A.	1961	Quinta revisión y sexto plan especial del proyecto de ordenación del Grupo montes de "Los Barrios" (decenio 1961-62 a 1970-71).
		Gallardo, J.	1975	Sexta revisión del proyecto de ordenación del Grupo de montes de "Los Barrios" nº 38 al 49 del catálogo de U.P. y séptimo plan especial (novenio 1971-72 a 1979-80).
Grupo de Montes de Algeciras (h)	1545	Illegible	1913	Revisión y proyecto de 2º plan especial en los "Montes de Algeciras" de la provincia de Cádiz.
		Castro, M.	1942	Segunda revisión del proyecto de ordenación del grupo de montes ordenados de los Propios de Algeciras y tercer plan especial.
		Castro, M.	1952	Tercera revisión y cuarto plan especial del proyecto de ordenación del Grupo de montes de Algeciras.
		Gallego, L.A.	1961	Cuarta revisión y quinto plan especial del proyecto de ordenación del Grupo de montes de Algeciras (decenio 1961-62 a 1970-71). Memoria Ordenación-Plan Especial.
		Junco, J.J.	1973	Quinta revisión del proyecto de ordenación del Grupo de montes de Algeciras, núms. 1 al 4 de catálogo de U. P. y 6º plan especial (convenio 1971-72 a 1979-1980).
Grupo de Montes de Tarifa (i)	14388	García, J.	1911	Proyecto de ordenación de los montes de Propios de Tarifa (Cádiz). Memoria.
		Atienza, F.	1919	Revisión reglamentaria del proyecto de ordenación del Grupo de Montes de Propios de Tarifa. Inventario, ordenación y segundo plan especial.
		Castro, M.	1946	Tercera revisión del proyecto de ordenación del Grupo de Montes de los Propios de Tarifa y cuarto plan especial.
		Rodenas, A.	1958	Cuarta revisión y quinto plan especial del proyecto de ordenación del Grupo de Montes del término y propios de Tarifa. Tomo 1º. Memoria.
		Junco, J.J.	1967	Quinta revisión del proyecto de ordenación del Grupo de Montes de Tarifa y sexto plan especial. Decenio 1964-65 a 1973-74. Memoria, ordenación y plan especial.
		Junco, J.J.	1976	Sexta revisión del proyecto de ordenación del Grupo de Montes de Tarifa nº 5 al 15 del catálogo de U.P. y séptimo plan especial. Novenio 1975 a 1983.

Appendix 3.2

Correlograms of *Q. suber*'s and *Q. canariensis*' abundance (raw data) at a landscape scale, (a) and (b), and residuals adding different explanatory variables to models (see landscape models in Table 3.1 and Fig. 3.5b). For *Q. suber*, distance to drainage, access-cost and altitude equivalently explained its abundance pattern (ΔAIC<2), but access-cost and altitude reduced the level of spatial autocorrelation at short distances (a). Correlograms of Moran's I showing patterns of spatial autocorrelation of *Q. suber*'s and *Q. canariensis*' abundance at a regional scale, (c) and (d), and residuals' autocorrelation after adding annual mean precipitation to models (see regional models in Table 3.2 and Fig. 3.6a).




(c) Q. suber
Raw
Annual P
Moran's I
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
0
50
100
150
200
250
300
Distance (km)


(d) Q. canariensis
Raw
Annual P
Moran's I
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
0
10
20
30
40
50
Distance (km)

Capítulo 4

Capítulo 4

Remoción de bellotas de *Quercus suber* y *Quercus canariensis*: consecuencias ecológicas del tamaño de semilla, de la cobertura vegetal y de la temporalidad en la caída de la bellota

Este capítulo reproduce el texto del siguiente manuscrito:

Pérez-Ramos, I.M., Urbieta, I.R., Marañón, T., Zavala, M.A. and Kobe, R.K. Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing. Oikos (in review).

Resumen

La depredación y dispersión de semillas son procesos que influyen de forma crítica en la estructura y dinámica de las comunidades vegetales. Las diferencias que aparecen durante estas fases tempranas entre las especies juegan un papel decisivo en los patrones de reclutamiento de las especies forestales, que posteriormente pueden influir en la dinámica del bosque y determinar la segregación de las especies en el paisaje, especialmente en ambientes heterogéneos como son los bosques mediterráneos. Se estudiaron las tasas de remoción de bellotas colocadas experimentalmente sobre un suelo forestal para dos especies mediterráneas de *Quercus, Q. canariensis* (quejigo moruno) y *Q. suber* (alcornoque), que coexisten al sur de la Península Ibérica. Se construyeron estimadores de máxima verosimilitud con el objetivo de explorar qué factores principales ejercían mayor influencia en las probabilidades de remoción de bellotas y cuáles eran las funciones de respuesta específicas de cada especie a estos factores. Se diseñaron dos tipos de experimentos para estudiar el efecto de las diferencias interespecíficas en la temporalidad en la caída de la bellota: experimentos sincrónicos, donde las bellotas de las dos especies se colocaron en el suelo al mismo tiempo, y experimentos diacrónicos, donde se simuló la fenología de cada especie colocando las bellotas en diferentes tiempos coincidiendo con el momento de su dispersión natural. Se colocaron experimentalmente un total de 1.536 bellotas a lo largo de un amplio gradiente natural de cobertura vegetal, y se monitorizó periódicamente su remoción durante tres meses en dos años consecutivos, en los que la producción natural de semillas de las dos especies y por tanto la disponibilidad natural de bellotas en el suelo varió enormemente. La probabilidad de remoción de las semillas de las dos especies se incrementó con la cobertura vegetal (LAI, leaf area index). Las diferencias en las tasas de remoción entre las dos especies fueron mayores en las zonas abiertas pero las tasas se igualaron en los microhábitats cubiertos, especialmente en un año no vecero. A pesar de que la caída de las bellotas de alcornoque es más tardía, sus bellotas fueron removidas más rápidamente y en mayor proporción que las bellotas de quejigo. Esto puede deberse al mayor tamaño de las bellotas de alcornoque, ya que al exponer semillas de las dos especies de similar tamaño y al mismo tiempo, las diferencias en las tasas de remoción entre las dos especies desaparecieron. Las diferencias entre las especies en la remoción de semillas debidas a la variabilidad de tamaños de semilla y a la heterogeneidad de los microhábitats a los que llegan, pueden ser de gran importancia en la diferenciación de nichos de las dos especies de estudio, y tienen importancia en la dinámica y composición de los bosques.

Seed removal in two coexisting oak species: ecological consequences of seed size, plant cover and seed-drop timing

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Abstract

Seed predation and dispersal critically influence plant community structure and dynamics. Inter-specific differences arising at these early stages play a crucial role on tree recruitment patterns, which in turn could influence forest dynamics and species segregation in heterogeneous environments such as Mediterranean forests. We investigated removal rates from acorns set onto the ground in two coexisting Mediterranean oak species - *Quercus canariensis* and *Q. suber* - in southern Iberian Peninsula. We developed maximum likelihood estimators to explore the main factors controlling probabilities of seed removal and to describe species-specific functional responses. To account for inter-specific differences in seed-drop timing, two experiments were established: a simultaneous exposure of acorns of the two species (synchronous experiments) and a seed exposure following their natural seed-drop phenology (diachronic experiments). A total of 1536 acorns were experimentally distributed along a wide and natural gradient of plant cover, and removal was periodically monitored for three months at two consecutive years (with contrasting differences in seed production and thus seed availability on the ground). The probability of seed removal increased with plant cover (leaf area index, LAI) for the two oak species. Inter-specific differences in acorn removal were higher in open areas and disappeared in closed microhabitats, especially during a non-mast year. Despite later seed-drop, *Q. suber* acorns were removed faster and at a higher proportion than those of *Q. canariensis*. The higher probability of seed removal for this species could be attributed to its larger seed size compared to *Q. canariensis*, as inter-specific differences were less pronounced when similar sized acorns were exposed. Inter-specific differences in seed removal, arising from seed size variability and microsite heterogeneity, could be of paramount importance in oak species niche separation, driving stand dynamics and composition along environmental gradients.

Keywords: failure time analysis; forest structure; heterogeneity; Mediterranean forest; seed dispersal; seed predation.

Introduction

Differential species requirements during the regeneration phase could contribute to species coexistence in plant communities (Grubb 1977). Differences between species can arise at any stage of the regeneration cycle, including flower fecundity and seed production, seed predation and dispersal, and seedling establishment, mortality and growth (Crawley *et al*. 1995). In large-seeded species such as temperate oaks, the seed-seedling transition plays a determinant role on tree recruitment. Once seeds reach the ground, a high proportion can be removed and consumed by predators, which usually translates into a major recruitment bottleneck for many forest tree species (e.g., Crow 1992; Herrera 1995; Santos and Tellería 1997; Gómez *et al*. 2003). Moreover, not all removed seeds are necessarily eaten, and the small proportion of acorns which are buried and not recovered by these animals (especially birds and rodents), acting as secondary dispersers, might be crucial for tree population dynamics (Díaz 1992; Gómez 2003; Purves *et al*. 2007). Therefore, inter-specific differences in this early phase can be critical for understanding initial tree recruitment patterns, which in turn largely drive forest composition and dynamics (e.g., Pacala *et al*. 1996; Zavala *et al*. 2000; Zavala and Zea 2004).

Differential preferences by seed predators and dispersers and how these preferences are influenced by environmental conditions could impact seed removal and thereby tree recruitment patterns. First, species-specific seed preferences could respond to differences in intrinsic traits of seeds, such as size, seed-coat thickness, content of defensive compounds or nutritional value (e.g., Robbins *et al*. 1987; Cipollini and Stiles 1991; Ganeshaiah and Shaanker 1991; Shimada and Saitoh 2003). Seed size has been attributed as one of the main characters affecting seed removal rates. All else being equal, larger seeds should experience greater predation than smaller seeds, since larger food items offer more energetic return for foraging effort (Janzen 1969; Harper 1977; Gómez 2004). On the other hand, larger seeds tend to have an increasing probability of being harvested and dispersed further away from the parent tree, thus with a positive effect of size on dispersal (see Jansen *et al*. 2004 and references therein). Nevertheless, preference by larger seeds is not an universal trend (Brewer 2001). Some authors have documented a higher success in the seed-seedling transition for seeds of intermediate (Theimer 2003) or smaller size (Brewer and Webb 2001), whereas others have not found any effect of this trait on seed removal rates (e.g., Xiao *et al*. 2004). In addition, seed preferences are manifested more strongly under higher seed abundance (Brewer 2001; Jansen *et al*. 2004; Theimer 2005). Therefore, the effect of seed size and how this trait influences the nature of plant-animal interactions appears to be influenced by several factors, including the study system, target species, as well as other external factors such as food availability.

With respect to temporal variability, the predator satiation (Janzen 1971; Silvertown 1980; Kelly and Sork 2002) and animal dispersal hypotheses (Ims 1990) suggest that the strong inter-annual variability in seed production (i.e., mast seeding; Silvertown 1980) commonly found in oak species, is an evolutionary response directed to minimize seed predation pressure, enhance success during seed dispersal and, thereby, favour seedling establishment during mast years (reviewed in Koening *et al*. 1994; Abrahamson and Layne 2003). These hypotheses could explain why coexisting species that share generalist seed consumers show synchronous masting (e.g., Schnurr *et al*. 2002). Since a species producing seeds out of synchrony may experience a higher probability of seed predation and a lower seedling recruitment (Janzen 1971; Ims 1990; Curran and Leighton 2000), even small inter-specific differences in seed-drop times may have an impor-

tant effect on the number of seeds that escape predation and that are successfully dispersed. However, the effect of among-species differences in the timing of seed-drop on the process of seed removal has been poorly studied.

Finally, seed removal can also vary spatially because predator and disperser foraging is not random (Clark *et al*. 1999; Jordano and Schupp 2000). Therefore, there may be a strong link between microhabitat structure and seed removal patterns, particularly in highly-heterogeneous landscapes such as Mediterranean forests (Rey and Alcántara 2000; Kolb *et al*. 2007).

In addition to the total number of seeds removed (either predated or dispersed), the rate at which seeds are removed can influence successful tree recruitment (Brewer 2001; Jansen *et al*. 2004). If a seed is cached and not relocated (successful dispersal), a shorter time to removal implies an earlier seedling emergence in the new location, which it is a major determinant of survivorship during the establishment phase (Nicotra *et al*. 2002). Conversely, if the seed is eventually consumed, the faster it is removed the lower the chance of germinating and emerging in the site where it was dropped, and thus the lower the probability to be independent from cotyledon reserves (Kennedy *et al*. 2004).

In this study, we investigated inter-specific variation in seed removal in two oak species - *Quercus canariensis* Willd. (Algerian oak) and *Q. suber* L. (cork oak) - in southern Iberian Peninsula (Aljibe mountains). In these mixed forests, acorn availability not only varies inter-annually (seed masting), but also intra-annually, due to small phenological differences in seed production and dispersal between the two oak species (Pérez-Ramos 2007). *Q. canariensis* acorns are dropped in September-December, whereas *Q. suber* acorns during October-February. Temporal variation in seed availability, which is generally lower in early autumn, could influence species preferences shown by acorn consumers. Accordingly, *Q. suber* acorns may be exposed to a lower removal pressure, but counteracting mechanisms, such as production of larger or more palatable seeds, could mitigate the potential effects of later seed-drop. To account for differences in seed-drop phenology, two experiments were established: a simultaneous exposure of acorns of the two species (synchronous experiments), and a seed exposure simulating their natural seed-drop phenology (diachronic experiments) during two consecutive years. Intra and inter-specific differences were evaluated by calibrating maximum likelihood estimators of acorn removal along a wide gradient of plant cover and seed sizes. Specifically, the main objectives were: (1) to examine the effect of seed size and plant cover on species-specific seed removal rates (both in percentage of the total of exposed acorns and taking into account their times to removal), (2) to investigate inter-specific variation in seed removal along gradients of these factors, (3) to evaluate the importance of species differences in seed-drop timing to removal rates, and finally (4) to discuss the ecological implications of these findings for forest stand dynamics and species coexistence.

Material and methods

Study area and species

The study was conducted in La Sauceda forest (530 m above sea level, 36º31´54´´ N, 5º34´29´´ W), located in the mixed oak forests of the Aljibe Mountains, near the Strait of Gibraltar, in southern Iberian Peninsula (see a detailed description of the experimental plot in Quilchano *et al*. 2008). The dominant bedrock in the area is Oligo-Miocenic sandstone, with rugged terrain and a highest peak of 1092 m a.s.l. The climate is sub-humid Mediterranean, with mild and wet winters, alternating with warm and dry summers. Annual mean temperature is 17 ºC, and annual mean rainfall is 1265 mm (1985-2004 data from La Sauceda meteorological station). Vegetation is dominated by evergreen cork oak (*Q. suber*) forests, mixed with winter deciduous oaks (*Q. canariensis*), which are more abun-

dant near streams (Urbieta *et al*. in press). The shrubby understorey is diverse and rich in endemic taxa (Ojeda *et al*. 2000). Most of the forested area has been protected within Los Alcornocales (meaning cork oak forests) Natural Park, covering about 1700 km^2. Large herbivores, such as red deer (Cervus elaphus), roe deer (Capreolus capreolus) and free-range cattle are abundant in this forest.

The fruits (acorns) of oaks usually have a single seed. *Q. suber* seeds are among the largest from Mediterranean tree species. Its seed production is restricted to the autumn/early winter season (between October and February) and there is strong inter-year variability. During the two sampling years of study (2003/04 and 2004/05 cycles), *Q. suber* acorn production was low (about 2.3 g/m^2/yr) in the study area (Pérez-Ramos 2007). *Q. canariensis* acorns are somewhat smaller than those of *Q. suber*, are dropped earlier (September-December), and exhibit strong inter-year variability in seed production; in this case, estimates of acorn production in the study area varied between 344.2 g/m^2 (2003/04 cycle) and 54.1 g/m^2 (2004/05 cycle) (Pérez-Ramos 2007). Although most acorns in both species are dropped onto the ground (which can be considered dispersal by gravity), a small number potentially could be dispersed by animals, mainly birds (e.g., Bossema 1979; Gómez 2003), rodents (e.g., Jensen and Nielsen 1986; Pulido and Díaz 2005) and even large insects such as dung beetles (Pérez-Ramos *et al*. 2007).

Experimental design and data collection

During their period of peak seed production and seed-drop (October-November for *Q. canariensis*, December-January for *Q. suber*), we collected acorns under several trees of each oak species to encompass intra-specific variation. We selected healthy, normal-sized acorns and discarded those infected by moth or beetle larvae using a flotation method (Gribko and Jones 1995). Selected acorns were stored on a moist vermiculite bed in plastic trays and kept at 2-4 ºC until their use in the experiment. Acorns were individually marked with a small spot of paint, and were randomly placed on the forest floor in a total of 192 experimental units (minimum distance of 10 meters relative to one another), evenly distributed along the vegetation cover gradient (see below), and labelled with small flags placed at half a meter distance to minimize attraction effects. Acorns were exposed on the surface of the floor, simulating the most common abiotic dispersal process (by gravity).

Experimental units spanned a wide and continuous gradient of plant cover, from open habitats (up to 90 % full sun, and Leaf Area Index - LAI - of 0.35), to deeper shade under shrubs and trees (down to 5 % full sun, 4.00 LAI). Plant cover was estimated by means of hemispherical canopy photographs taken in the centre of each experimental unit in winter (December-January), using a horizontally-levelled digital camera (Coolpix 4500, Nikon, Tokyo, Japan) with a fish-eye lens of 180º field of view (FCE8,

Table 4.1 Experimental design scheme for each sampling year.

	2003-2004	**2004-2005**
Type of experiments	DI (diachronic)	DI and SYN (synchronous)
Censuses	24h, 7d, 15d, 30d, 60d, 100d	7d, 30d, 100d
Factors measured	LAI	LAI and seed weight
Mean seed production	*Qsub* : 2.3 g/m^2	*Qsub* : 2.3 g/m^2
	Qcan : 344.2 g/m^2	*Qcan* : 54.1 g/m^2
Mean ± SD seed weight		*Qsub* : 5.96 ± 2.20 g; (2.31-17,27 g)
		Qcan : 2.57 ± 1.03 g; (0.91-8.29 g)

Nikon) (see details in Valladares and Guzmán 2006; Quilchano *et al*. 2008). We used Hemiview Canopy Analysis software (Delta-T Devices Ltd. 1999, v. 2.1) to analyse the images and to calculate Leaf Area Index (LAI), which was selected as the most representative measure of plant cover. Global Site Factor (GSF, i.e., percentage full sun) and LAI were highly correlated ($r = -0.80$, $p<0.001$).

In order to evaluate the effect of seed-drop timing on seed removal rates, two sets of experiments were carried out: an exposure of seeds simulating the typical phenology of each species (diachronic experiments, DI) and a simultaneous exposure (synchronous experiment, SYN) (see Table 4.1).

Diachronic experiments (DI)

During the peak seed-drop period of each species, 576 acorns (including both species) were placed during each of the two reproductive cycles, 2003-2004 and 2004-2005 (hereafter DI 03-04 and DI 04-05), across 144 experimental units distributed along a wide and continuous plant cover gradient (see description above). *Q. canariensis* acorns were first placed in mid October (2003) or early November (2004), while *Q. suber* acorns were exposed in the field in early December (2003 and 2004) in neighbouring units, so that there was no interference between the two species. In each unit, four acorns (without cupule) per species were placed on the ground, in the corners of a 0.5 m^2 quadrat.

Units were periodically visited and acorns individually monitored until there was no longer any evidence of seed removal (approximately after three months). On each visit, the status of the acorn (unaffected, removed, or consumed in situ) was recorded. During the first cycle, censuses were carried out at 24 hours, 7 days, 15 days and then monthly (up to 3 months). For the second cycle, three censuses were made, elapsing 7 days, 1 month and 3 months. This approach allowed us to calculate the time elapsing until each experimental acorn was removed. Those acorns remaining unaffected at the end of the experiment were considered as right-censored data. Despite different start dates of acorn placement for the two species, both of them remained exposed to predators and dispersers for the same number of days (up to 100), providing comparable experimental treatments. All experimental acorns, during the second year, were individually weighed to the nearest 0.01g. Mean ± SD (standard deviation) acorn fresh weight (g) was: 5.96 ± 2.20 for *Q. suber* (range of 2.31-17.27g, n=576) and 2.57 ± 1.03 for *Q. canariensis* (range of 0.91-8.29g, n=576). Acorn fresh weight was used in the analyses as a surrogate of seed size.

Synchronous experiment (SYN)

Acorns of the two species were placed in the field simultaneously in a synchronous experiment that was carried out in the second reproductive cycle, during late November 2004 (hereafter SYN 04-05), following a similar experimental design. Acorns were experimentally exposed when seed-drop periods of the two oak species overlapped, in order to test whether animals preferred one of the species, excluding the effect of differential seed-fall phenology. Moreover, in this case, acorns of similar mass (i.e., within the same range of seed sizes) were selected for both species in order to remove any possible seed size effect on animal selection. Acorns of both species were mixed and placed at the same time across 48 dispersal units, distributed along the plant cover gradient, with four acorns (two per species) intermixed on each quadrat (total of 192 acorns). Three censuses were made (after 7 days, 1 month and 3 months), recording the status of the acorn (unaffected, removed or consumed in situ).

Data analysis

Using maximum likelihood techniques, we fitted linear and non-linear models of acorn removal for each species using two complementary approaches. First, we considered a binomial experiment with each independent trial resulting

in just two possible final outcomes, i.e., seed manipulated by animals (removed or consumed in situ) or unaffected after three months of exposure on the forest floor. Since only a small proportion of acorns (below 10%) were consumed in situ, hereafter we refer to manipulated seeds simply as removed. Second, we conducted a failure time analysis (Pyke and Thompson 1986) to evaluate explicitly the time elapsing until a seed was removed. In both approaches, the final (i.e., after three months of exposure) removal probabilities were calculated for each species. However, we will focus on the results obtained by failure time analyses, which captured biologically meaningful responses that were masked by the binomial approach, particularly when seed removal rates at the end of the experiment were very high (see Appendix 4.1 for an explicit comparison of the two statistical methods). Failure time analysis considered not only the final "fate" of each seed (i.e., removed or not), but also the time each seed remained non-removed, thus providing greater temporal resolution in removal rates which could be critical for the regeneration of these species. Since most non-removed acorns germinated during the census intervals, we considered the probability of surviving until germination.

For each oak species, we specified the hazard function as function of LAI and/or seed size (both as continuous variables), fitting several functional responses that covered a wide range of forms: linear, exponential, power and logistic (see Table 4.2 for equations). This modelling approach is suitable to identify strategic axes along which species differentiate (e.g., Pacala *et al*. 1996; Kobe 1999). Specifically, removal models along the plant cover gradient (LAI) were developed for DI 03-04 and SYN 04-05 experiments. For DI 04-05, when individual seed sizes were available, we specified removal models as functions of LAI and seed size.

Models were parameterised with maximum likelihood (Edwards1992), using a simulating anneaing algorithm (Metropolis *et al*. 1953; Chib and Greenberg 1995). To test for the influence of predictors (seed size and LAI) in seed survival, fitted models were compared to a null model of no factor effect using Likelihood Ratio Tests (LRTs) (Edwards, 1992). To analyze inter-specific differences, 95% support regions (equivalent to 95% confidence intervals but used in conjunction with likelihood methods) were also estimated by the likelihood profile method (Hilborn and Mangel 1997). When species-specific parameter 95% support regions did not overlap, differences between species were considered to have empirical support. Fitted models were compared with Akaike's Information Criteria, specifically ΔAIC, which is defined for each $Model_i$ as: AIC_i - $AIC_{minimum}$ (Akaike 1992). The model with the strongest empirical support has the minimum AIC and thus, ΔAIC= 0. Models with ΔAIC between 0-2 were considered to have equivalent and substantial empirical support, ΔAIC between 4-7 indicated less support and models with ΔAIC >10 were dismissed as they had negligible empirical support (Burnham and Anderson 2002). All the models and numerical algorithms were implemented in programs we wrote in C (Borland International Inc. 1996 v.5.01).

Results

Experimentally dispersed *Q. canariensis* and *Q. suber* acorns experienced high removal rates in both years of study. In all cases, the probability of seed removal increased exponentially with plant cover (LAI) and seed size for the two oak species (Tables 4.2, 4.3, 4.4). Inter-specific differences, however, varied among years and between diachronic and synchronous experiments (see below).

Diachronic experiments (DI)

In the diachronic experiments (DI 03-04 and DI 04-05), *Q. suber* acorns had a higher removal probability than *Q. canariensis*, despite their later placement on the forest floor. In both species, removal rates increased exponentially with LAI according to best model fits (i.e., ΔAIC=0) (Tables 4.2, 4.3). This was especially noticeable during DI 03-04, when both species markedly

Table 4.2 Maximum likelihood parameter estimates for acorn removal models of each species during DI 03-04 (diachronic experiment).

DI 03-04	Factor	Best fit	A	S	Log.Like	LRT ($\times^2$)	p	d.f	AIC	Δ AIC
Q.can	LAI	Expon.	0.138	0.529	-391.4	24.9	***	1	786.9	**0.0**
	LAI	Logistic	-1.840	0.701	-393.0	21.8	***	1	790.0	3.1
	LAI	Linear	0.121	0.134	-394.0	19.8	***	1	792.0	5.1
	LAI	Power	0.262	0.583	-395.7	16.3	***	1	795.4	8.6
	Null model				-403.9				809.8	22.9
	Factor	**Best fit**	**A**	**S**	**Log.Like**	**LRT ($\times^2$)**	**p**	**d.f**	**AIC**	**Δ AIC**
Q. suber	LAI	Expon.	0.139	0.975	-318.9	126.4	***	1	641.8	**0.0**
	LAI	Power	0.421	1.313	-327.6	109.0	***	1	659.2	17.4
	LAI	Linear	-0.044	0.502	-330.1	104.0	***	1	664.2	22.4
	LAI	Logistic	-1.999	1.657	-338.5	87.2	***	1	681.0	39.2
	Null model				-382.1				766.2	124.4

Note: Models are ranked from best to poorest fits. A and S are parameter estimates that maximized the likelihood function, and $Factor_i$ are the measured predictor variables for each acorn 'i'. The hazard function can take different forms as expressed in the equations below. LogLike. corresponds to the maximum log-likelihood: log(Lq|data, model). AIC (Akaike's Information Criteria) is calculated as: AIC = -2log(Lq|data, model) + 2K, being K the number of parameters in the model. Model fits are evaluated through loglikelihood ratio test (LRT, *p<0.05, **p<0.01, ***p<0.001) and ΔAIC ($AIC_i - AIC_{min}$). Bold font denotes models with equivalent empirical support (i.e., ΔAIC<2).

Linear: $A + SFactor_i$ Exponential: $Ae^{(SFactor_i)}$ Power: $AFactor_i^{\ S}$ Logistic: $\frac{e^{(A+SFactor_i)}}{1+e^{(A+SFactor_i)}}$

Table 4.3 Maximum likelihood parameter estimates for acorn removal models of each species as function of plant cover (LAI) and seed size, during DI 04-05 (diachronic experiment).

DI 04-05	Factor 1	Factor 2	Best fit	A	S	D	Log.Like	LRT ($\times^2$)	p	d.f	AIC	ΔAIC
Q.canariensis	LAI	Seed size	Expon.+	0.292	0.687	0.095	-250.8	60.9	***	2	507.7	**0.0**
	LAI		Expon.	0.366	0.702		-252.2	58.2	***	1	508.4	**0.7**
	LAI		Linear	0.243	0.575		-259.2	44.2	***	1	522.4	14.7
	LAI	Seed size	Expon.*	0.586	0.764	0.177	-261.0	40.6	***	2	528.0	20.3
	LAI		M.Menten	1.999	1.538		-268.2	26.2	***	1	540.3	32.6
	LAI		Logistic	-0.125	1.546		-275.6	11.3	***	1	555.3	47.6
	LAI		Power	-0.123	1.546		-275.6	11.3	***	1	555.3	47.6
	Seed size		Expon.	0.628	0.160		-277.7	7.2	**	1	559.4	51.7
	Seed size		Linear	0.592	0.143		-278.2	6.1	*	1	560.5	52.8
	Null model						-281.3			1	564.6	56.9
	Factor 1	**Factor 2**	**Best fit**	**A**	**S**	**D**	**Log.Like**	**LRT ($\times^2$)**	**p**	**d.f**	**AIC**	**ΔAIC**
Q. suber	LAI	Seed size	Expon.+	0.581	0.415	0.043	-172.1	47.1	***	2	350.1	**0.0**
	LAI		Expon.	0.757	0.410		-173.2	44.9	***	1	350.4	**0.2**
	LAI	Seed size	Expon.*	0.906	-0.079	-0.61	-174.7	41.8	***	2	355.4	5.2
	LAI		Linear	0.867	0.371		-177.0	37.2	***	1	358.0	7.9
	Seed size		Expon.	1.123	0.034		-182.3	26.7	***	1	368.5	18.4
	Seed size		Linear	1.113	0.045		-182.3	26.6	***	1	368.7	18.5
	Seed size		M.Menten	1.212	-1.999		-184.0	23.3	***	1	372.0	21.8
	Null model						-195.6			1	393.2	43.1

Note: Models are noted and evaluated as in Table 4.2 and ranked from best to poorest fits. A and S are parameters estimates that maximized the likelihood function. D is the estimated parameter when Factor 2 was added to the functional response that yielded the best fit when evaluated singly. Additive interactions between two factors are noted as (+) and multiplicative as (*).

differed along most of the plant cover gradient, with an overlap of 95% support regions just in the extremes of the LAI gradient (Fig. 4.1).

In open areas (low LAI), the two species had similar removal probabilities (p=0.4-0.5). For intermediate values of plant cover, *Q. suber* acorns always experienced higher removal rates than *Q. canariensis*, whereas in more shaded areas (with denser vegetation) acorns of both species were virtually all removed.

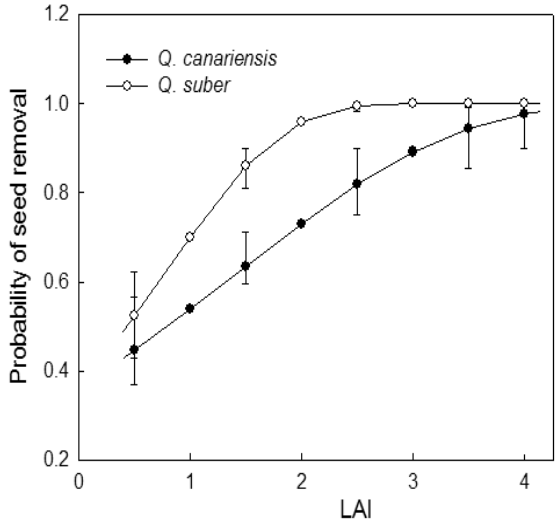

Figure 4.1 Models resulting in the best fit for acorn removal along a plant cover gradient (expressed by Leaf Area Index, LAI), with 95% support regions, during DI 03-04 experiment. Final seed removal probabilities (after three months of exposure on the forest floor) increase differently with LAI for both oak species.

During DI 04-05, seed removal rates were higher than in the previous year for both species (final mean removal of 93%). Again, seed removal rates varied with LAI, which had the strongest empirical support for inclusion in the models (Table 4.3). Removal increased with LAI for both species, and reached values close to one along a large part of the plant cover gradient. Only in the most open areas (with low LAI), did seeds have some chance to escape from animals, especially those with a smaller size (Fig. 4.2a), as indicated by the best-supported models (ΔAIC= 0) for both species (Table 4.3).

For a mean value of seed weight (i.e., 5g), *Q. suber* acorns had higher removal probability along the plant cover gradient than those of *Q. canariensis*, although inter-specific differences were only noticeable for very low values of LAI (Fig. 4.2b). In these open areas (i.e., LAI=0.5), probability of seed removal also increased with seed size in both oak species, with a more pronounced effect for *Q. canariensis* (Fig. 4.2c). *Q. canariensis* acorns (range of 0.9-8.3 g) were in general smaller than those of *Q. suber* (2.3-17.3 g), and overall had a lower removal rate. However, in the common interval of acorn size for both species (2.5-8 g), the 95% support regions overlapped and thus, species did not differ (Fig. 4.2c).

Table 4.4 Maximum likelihood parameter estimates for acorn removal models of each species along the plant cover gradient, during SYN 04-05 (synchronous experiment) using failure time approach.

SYN 04-05	Factor	Best fit	A	S	Log.Like	LRT ($\times^2$)	p	d.f	AIC	Δ AIC
Q. can	LAI	Expon.	0.4934	0.5826	-79.10	11.4	***	1	162.2	**0.0**
	LAI	Linear	0.5515	0.4272	-81.09	7.5	**	1	166.2	4.0
	LAI	Power	1.0077	0.4503	-82.60	4.4	*	1	169.2	7.0
		Null			-84.82					
	Factor	**Best fit**	**A**	**S**	**Log.Like**	**LRT ($\times^2$)**	**p**	**d.f**	**AIC**	**Δ AIC**
Q. suber	LAI	Expon.	0.7432	0.3801	-68.67	9.7	**	1	141.3	**0.0**
	LAI	Linear	0.7890	0.3580	-69.39	8.3	**	1	142.8	1.4
	LAI	Power	1.1901	0.2898	-70.30	6.5	*	1	144.6	3.3
		Null			-73.55					

Note: Models are ranked from best to poorest fits and evaluated as in Table 4.2.

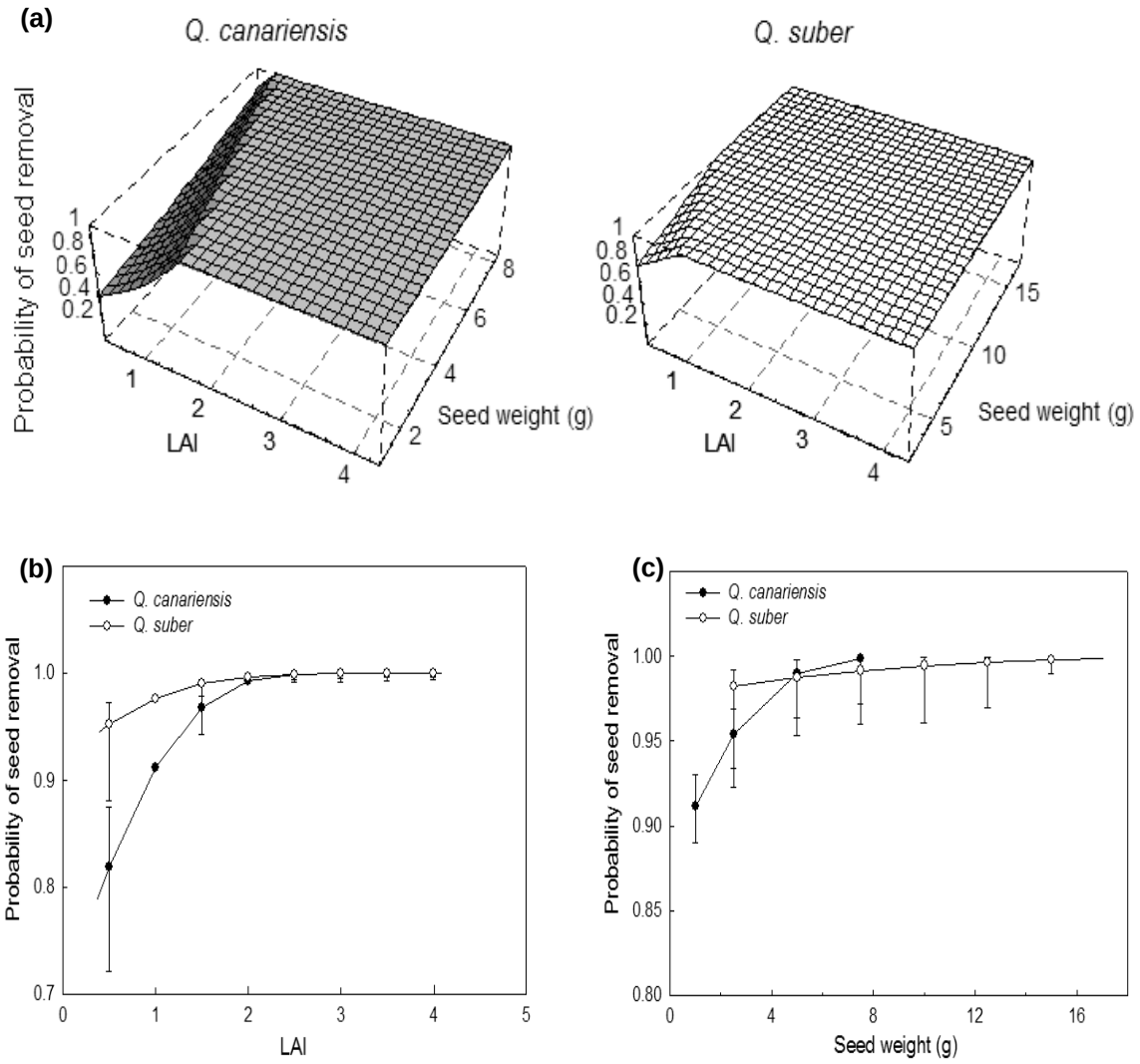

Figure 4.2 (a) Models resulting in the best fit for acorn removal as function of plant cover (Leaf Area Index, LAI) and seed weight (g), with 95% support regions, during DI 04-05 experiment. Final seed removal probabilities increase with LAI and seed weight for both oak species. Notice different scales in the axes. (b) Inter-specific differences in removal probabilities along the plant cover gradient for an average seed weight of 5g. (c) Inter-specific differences in removal probabilities as function of seed weight for a given point of the plant cover gradient (LAI= 0.5).

Synchronous experiment (SYN)

The importance of seed size on removal probabilities was supported by the synchronous experiment, in which acorns of both species with similar weight were exposed on the ground at the same time. The two oak species experienced very high seed removal rates (approaching 100%) with overlapping support regions at all LAI values; thus, there were no differences between them along the plant cover gradient (Fig. 4.3). In this case, removal probabilities also increased with LAI for both species (Table 4.4).

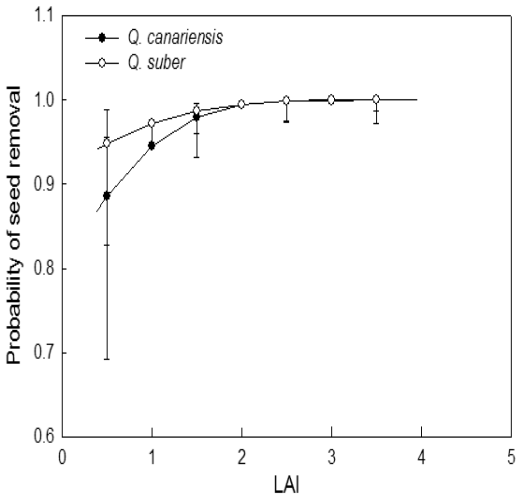

Figure 4.3 Models resulting in the best fit for acorn removal as function of plant cover (Leaf Area Index, LAI), with 95% support regions, during SYN 04-05 experiment, where both oak species´ seeds with similar weights were experimentally dispersed at the same time.

Discussion

Factors influencing intra- and inter-specific differences in seed removal

Our results show divergence in seed removal rates for two co-occurring oak species. Despite their later seed-drop, *Q. suber* acorns were removed faster and with higher probability in comparison with *Q. canariensis* ones. These differences, however, varied among years and along plant cover and seed size gradients.

Seed removal was strongly affected by the type of microhabitat where the acorn was placed, highlighting the relevance of environmental variables as mediators of plant-animal interactions (Kolb *et al*. 2007). Probability of seed removal increased under denser plant cover (i.e., higher LAI values) for both oak species. This positive relation is usually attributed to the action of small rodents, which show a higher activity in more closed microhabitats, where they find more protection against their predators (Kikuzawa 1988; Herrera 1995; Hulme and Kunt 1999; Gómez *et al*. 2003).

Seed removal patterns of both species varied between the two sampled years, likely arising from variable acorn production between reproductive cycles, which led to variable food resources (acorns) for seed consumers on the forest floor. During the first cycle 2003-04, the estimated seed production (especially of *Q. canariensis*) was very high. In the diachronic experiment (DI 03-04), *Q. canariensis* acorns (that were sown earlier) were removed less by animals than those of *Q. suber*, along most of the vegetation cover gradient. The high availability of resources (acorns) may have resulted in seed-predator satiation (Janzen 1971; Crawley and Long 1995; Wolf 1996) and species-specific seed preferences may have been more perceptible (Jansen *et al*. 2004). In contrast, during the second cycle (2004-05), estimated seed production of both species was very low, and removal probabilities of experimental seeds approached 100%. Under food scarcity, animals are usually less selective because they need a greater percentage of seeds to build up enough reserves for surviving the next season (Jansen *et al*. 2002). In this case, inter-specific differences were only perceptible in open areas, where rodents probably selected more attractive food (*Q. suber* acorns) to compensate for the risk.

In the range of plant cover where inter-specific differences were significant, *Q. suber* acorns were always removed faster and at a higher proportion than *Q. canariensis* acorns, independent of seed availability on the forest floor. In

fact, in another forest site within the study area, Pérez-Ramos and Marañón (unpublished data) also found a higher preference for acorns of this species, even when the estimated seed production of *Q. suber* was higher than *Q. canariensis*. These results do not support the initial hypothesis proposing a lower removal risk for *Q. suber* acorns due to their later seed-drop phenology and later availability for animals (assumed as being satiated with the earlier available *Q. canariensis* acorns), but instead suggest the likely influence of other factors related to specific characteristics of *Q. suber* acorns. Differences in seed removal between the two oak species here seem to be mostly a consequence of seed size variation. Overall, *Q. suber* acorns were bigger than those of *Q. canariensis* and this was probably the main cause of being removed faster by rodents. Indeed, both in synchronous and diachronic experiments, inter-specific differences in removal rates were not significant when a similar seed size range was explored. Therefore, although seed removal rate for *Q. suber* likely was reduced due to its delayed seed-drop phenology, the higher size of acorns makes them more attractive for animals than *Q. canariensis* ones.

At the intra-specific level, the probability of seed removal also increased with seed weight in both species, consistent with previous studies (e.g., Moegenburg 1996; Gómez 2004; Jansen *et al*. 2004). However, the influence of seed size on inter-specific differences contrasts with other studies where this trait did not exert any significant effect (Xiao *et al*. 2004), or the species was the most influential factor on animal selection (Hulme and Borelli 1999; Pons and Pausas 2007a, 2007b). In any case, differences in seed quality between *Q. suber* and *Q. canariensis* acorns, independently of size, should also be investigated. Although a previous seed chemical analysis showed that nutritional content was similar in acorns of both oak species (Pérez-Ramos 2007), inter-specific differences in defensive compounds (e.g., tannins), not yet analysed, could play an important role (Shimada and Saitoh 2003).

Implications of seed removal for forest stand dynamics

Seed removal of the two oak species - *Q. canariensis* and *Q. suber* - was very high during the two years of study. In just three months, a large proportion of experimental acorns placed onto the ground were removed by animals; thus, seed-seedling transition could be an important bottleneck in regeneration of the studied oaks, as has been documented for other species (Crow 1992; Herrera 1995; Santos and Tellería 1997; Gómez *et al*. 2003). A high proportion of acorns removed by the different seed harvesters (mostly rodents) are relocated and eaten later (Bossema 1979; Kikuzawa 1988; Iida 1996; Kollmann and Schill 1996). However, it is likely that a small fraction escapes consumption, in which case mice act as secondary dispersers (Jensen and Nielsen 1986; Pulido and Díaz 2005). A similar interaction was documented for dung beetles (*Thorectes lusitanicus*) in the same forest site; interestingly they bury but do not always eat *Q. canariensis* and *Q. suber* acorns (Pérez-Ramos *et al*. 2007). Thus, the small proportion of buried, surviving seeds discarded or forgotten by these scatterhoarder animals at safe sites might also be crucial for long term viability of oak populations (e.g., Díaz 1992; Gómez 2003; Purves *et al*. 2007). The outcome of plant-scatterhoarder interaction can shift along a continuum from antagonistic (seed predation) to mutualistic (seed dispersal) relations (Bronstein 1994), and this conditional mutualism mostly depends on the relative abundance of seeds versus that of scatterhoarders (Theimer 2005). At low seed/scatterhoarder ratios, rodents act mainly as antagonistic predators, whereas at high values (for example, during mast years) rodents act more as dispersers and less as seed predators (Theimer 2005).

Since the main differences between the two co-occurring species (among several regeneration stages) were observed precisely during the seed-seedling transition (Pérez-Ramos 2007), our modelling approach could help elucidate

how overall recruitment of both species varies in the landscape. The ecological implications of inter-specific differences for forest stand dynamics and species coexistence will likely depend on the nature of plant-animal interactions, which are partly determined by food (seed) availability (Jansen *et al*. 2004), and environmental heterogeneity of the particular site. Accordingly, during a year of low seed production (such as 2004-05 in the study area), most removed acorns are likely consumed later and then *Q. canariensis* could gain an advantage over *Q. suber* and even replace it in certain microhabitats. In contrast, under high seed abundance (such as 2003-04) greater food availability likely satiates seed predators (Janzen 1971; Silvertown 1980; Kelly and Sork 2002), and a larger proportion of removed acorns are cached and probably not relocated later (successful dispersal). In this situation, *Q. suber* could be favoured over *Q. canariensis* due to the fact that their acorns are clearly preferred by animals (potential dispersers) as a consequence of their bigger size.

It is important to highlight that the differences found between the two oak species were consistent across most of the plant cover gradient, especially during mast years. However, in more closed microhabitats located under several shrub and tree layers, seed removal was very high for both species (probably also predation rates) and, combined with the strong light limitation for emerged seedlings, almost no recruitment will be expected in that type of microhabitat. These results are consistent with previous studies (e.g., Pons and Pausas 2006) but contrast with the documented effect of shrubs as protectors of tree seedlings from herbivores under Mediterranean conditions (Gómez 2003; Castro *et al*. 2004; Pulido and Díaz 2005). On the contrary, the probability of seeds escaping from animal removal was higher in open microhabitats for both oak species, but conditions for seed germination and establishment of seedlings were less suited in this type of microhabitat, due to soil waterlogging during the wet season (chapter 5, Urbieta *et al*. unpublished). Thus, there seems to be a conflict between demographic stages (sensu Schupp 1995); microhabitats with a low removal risk for seeds may exhibit less favourable conditions for subsequent seedling recruitment, and vice versa. Therefore, spatial patterns of seed removal, as a result of the activity and habitat use of seed predators and dispersers, as well as their preferences for acorns of certain species, may have strong influence on tree regeneration and landscape forest dynamics (López-Barrera *et al*. 2005; Purves *et al*. 2007). Biotic and abiotic factors may operate synergistically to result in critical seedling recruitment episodes. Understanding how feedbacks between rodent abundance, seed production, disturbances and rainfall variability modulate tree recruitment are critical to developing realistic and mechanistic models of forest dynamics under Mediterranean conditions.

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Appendix 4.1

Binomial vs. failure time analysis

From a statistical point of view, this study could be used as an interesting example of the comparison between two common types of analyses applied in seed removal studies. Most studies only consider the final seed removal rate, treating the dependent variable as a binomial, i.e., with each independent trial resulting in just two possible final outcomes: a seed manipulated by animals or unaffected. However, the inclusion of survival times can provide more relevant information, as documented in the present case study. Failure time analyses allowed us to detect the effect of LAI and seed size, which remained masked by using the binomial approach (Fig. 4.4). This was especially noticeable in those situations where the overall seed removal was very high, such as in DI 04-05, when resource availability was scarce and likely seed consumers density very high. However, seed survival times statistically differed as function of seed size and depending on where seeds were dispersed (plant cover). This could have important implications if we treat species recruitment as a dynamic process, in which the time elapsing from seed dispersal until the seed is removed by animals can affect its capacity to establish as a seedling (see Introduction section for the importance of time to removal, and Data analysis section for statistical details of both methods).

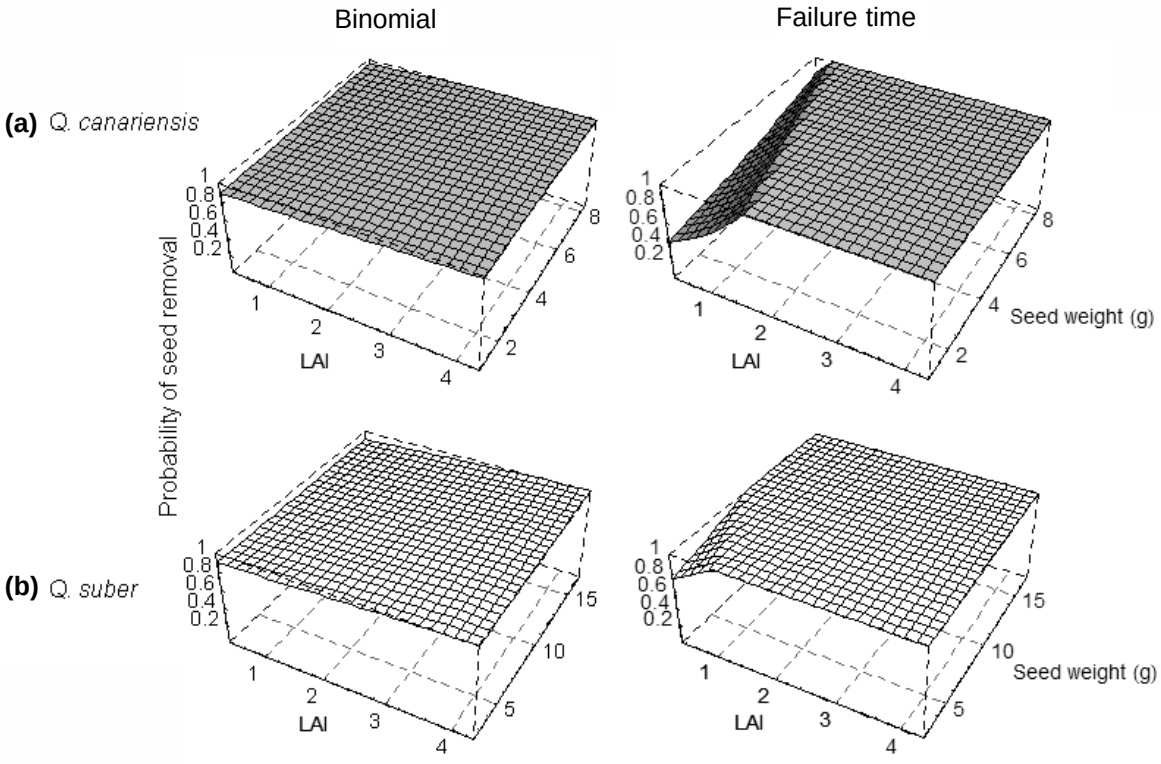

Figure 4.4 Models resulting in the best fit for seed removal of both species, *Q. canariensis* (a) and *Q. suber* (b), during DI 04-05. Notice different scales in the axes. Binomial and failure time approaches are compared. No effect of seed size nor LAI were captured when assuming a simple binomial, whereas introducing "survival times" we observed that in open areas (low LAI) seeds "survived" longer without being manipulated by seed predators or dispersers (especially smaller ones), with important ecological consequences for tree recruitment.

Capítulo 5

Capítulo 5

La heterogeneidad del agua en el suelo y el tiempo de emergencia controlan el establecimiento de plántulas de tres especies de *Quercus*

Este capítulo reproduce el texto del siguiente manuscrito:

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Resumen

La diferente respuesta de las especies arbóreas a la disponibilidad de recursos durante la fase crítica de establecimiento de plántulas puede influir en la dinámica forestal. Los estudios en bosques mediterráneos se han centrado fundamentalmente en el análisis de los efectos de la sombra y de la sequía estival en la supervivencia de plántulas. Sin embargo, no se conocen los efectos de las lluvias que caen desde el otoño hasta la primavera sobre las etapas más tempranas (germinación y emergencia) del reclutamiento de plántulas. A tal fin, se llevó a cabo un experimento de siembra de bellotas a lo largo de gradientes naturales de disponibilidad de luz y agua (durante los periodos húmedo y seco) con tres especies de *Quercus* (*Q. suber*, *Q. canariensis*, *Q. pyrenaica*) que coexisten y que muestran una limitada regeneración natural al sur de la Península Ibérica. Las etapas del reclutamiento de plántulas se monitorizaron durante un año. Se construyeron modelos de germinación, emergencia y supervivencia (por máxima verosimilitud) para cada especie en función de la luz, el contenido de agua en el suelo durante la época húmeda y seca, y la compactación del suelo. También se analizó la influencia de la variación intraespecífica del tamaño de la semilla y de los tiempos de emergencia en cada fase. Los resultados muestran que el exceso de agua en el suelo durante el invierno (debido a las fuertes lluvias) causó una menor germinación y emergencia de plántulas sobre todo en las zonas más abiertas y encharcadas. Asimismo, el encharcamiento provocó un retraso en el tiempo de emergencia de las plántulas, lo que se tradujo en una menor probabilidad de supervivencia durante la época seca. Por tanto, durante el establecimiento de plántulas el agua actuó como un doble factor de estrés: por exceso en la época lluviosa y por defecto en la época seca. En general, un mayor tamaño de semilla contribuyó a una mayor probabilidad de germinación y emergencia de plántulas. Estos resultados muestran que la heterogeneidad temporal y espacial del contenido de agua en el suelo, mediada por los tiempos de emergencia de plántulas, juega un papel determinante en la dinámica de la regeneración de los bosques mediterráneos de *Quercus*.

Soil water heterogeneity and emergence time control seedling establishment in three co-occurring oak species

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Abstract

Tree species can differ in their responses to resource availability during the critical phase of establishment, which could influence forest dynamics. In Mediterranean forests, most of the attention has focused on the effects of shade and summer drought on seedling survival, but little is known about the effect of autumn to spring rains on earlier stages of recruitment (germination and emergence). A sowing experiment was set up along natural gradients of light availability and water content (during wet and dry periods) with three co-occurring oak species (*Quercus suber*, *Q. canariensis* and *Q. pyrenaica*), that show limited natural regeneration in the south of the Iberian Peninsula. Recruitment stages were monitored for one year. Using maximum likelihood, models of germination, emergence, and survival were developed as functions of light, soil moisture during wet and dry periods, and soil compaction. The influence of intra-specific variation in seed mass and emergence time were also tested. Over-abundant soil water levels during the winter (due to heavy rains) reduced germination and emergence and lengthened time to emergence (in waterlogged open areas), which in turn decreased seedling survivorship during the dry season. Thus, water acted as a double factor of stress (by excess and deficit) during seedling establishment. Seedlings from larger seeds had overall increased probabilities of germination and emergence. Results suggest that temporal and spatial heterogeneity of soil water content, mediated by emergence time and seed size, play a crucial role in the regeneration dynamics of Mediterranean oak forests.

Keywords: light heterogeneity; Mediterranean forest; *Quercus suber*; regeneration niche; resource effect; seed germination; seedling survival; waterlogging.

Introduction

Resource competition and stress tolerance are important drivers of plant community structure and dynamics (Grime 1979; Tilman 1982). Plant species can differ in their responses to both resource abundance and scarcity during the critical phase of establishment (Sher *et al*. 2004). Differences in regeneration requirements and responses to environmental heterogeneity define regeneration niches that influence community composition (Grubb 1977; Beckage and Clark 2003). Therefore, the assessment of stress tolerance and survival in early stages of life cycles and during periods of resource variability could be important to understand forest community dynamics.

In seasonally dry environments, rainfall is too scarce to support the closed canopy that normally drives plants to compete for light; instead belowground resources such as water and nutrients can be more limiting (Coomes and Grubb 2000). Rainfall variability coupled with site factors such as microtopography, soil type, or vegetation cover, translate into a spatially and temporally heterogeneous soil moisture content, that can provide axes of ecological differentiation among species (Joffre and Rambal 1993; Chesson and Huntly 1997). In Mediterranean ecosystems, for example, interactions among water and light availability can lead to differential regeneration strategies in tree species in response to variability in these factors (Sack 2004; Sánchez-Gómez *et al*. 2006), thereby influencing forest composition and dynamics (Zavala and Zea 2004). Most of the attention in Mediterranean forests has centred on the effects of water shortage on forest regeneration. In particular, summer drought is commonly thought to be a major limiting factor for seedling survival (Espelta *et al*. 1995; Pulido and Díaz 2005), with shade conditions alleviating drought stress in seedlings, but potentially leading to light limitation (Quero *et al*. 2006). Nonetheless, effects of wet-period rains, which could be a critical bottleneck to earlier stages of recruitment (i.e., seed germination and emergence), remain rather uncertain.

Predictions of forest regeneration patterns must account for discordant microsite effects on seedling recruitment stages (Jordano and Herrera 1995), since environmental conditions that are optimal during one stage can be sub-optimal for others, causing demographic conflicts (Schupp 1995). The timing of seasonal precipitation and the wide range of light conditions in the understorey of Mediterranean forests, require quantitative studies that match detailed demographic sequences of seedling establishment with fine-scale spatiotemporal variation in resources. In this study, we conducted a sowing experiment of three co-occurring Mediterranean oaks, *Quercus suber* L. (cork oak), *Q. canariensis* Willd., and *Q. pyrenaica* Willd., along field gradients of water and light, with emphasis on wet and dry period water effects on seedling recruitment stages (from seed germination to one-year establishment). We focused on the most southern European oak forests (mountains north of the Strait of Gibraltar). Natural dynamics have been little studied, but both oak seedlings and saplings are scarce. All yearly rainfall concentrates from autumn to spring (causing frequent soil waterlogging locally), followed by a pronounced summer drought. Thus, this ecosystem provides a natural model system for examining the effects of three important and widespread environmental drivers for vegetation, i.e., drought, waterlogging, and shade, on forest regeneration [see Niinemets and Valladares (2006) for a review of these factors of stress].

Specifically, recruitment stages (germination, emergence and one-year seedling survival) of oaks were monitored regularly. Seed mass can influence seedling performance during early establishment (Seiwa 2000) and thus was treated as a covariate in our analyses. In addition, seedling emergence time was monitored, because together with strong seasonality in pre-

cipitation, emergence time could influence survival and hence plant fitness (Verdú and Traveset 2005). We calibrated species-specific models of seed germination, seedling emergence and survival, in order to address the following questions: (1) How do contrasting soil water availability (during wet and dry seasons) and light availability in the understorey influence the success of oak species during each recruitment stage (germination, emergence and survival)? (2) Could local waterlogging produced by autumn to spring rains reduce oak regeneration? (3) Do initial seed mass and emergence timing mediate responses to light and water heterogeneity? (4) Over gradients of resource availability, do co-occurring oak species differ in their response?

Material and methods

Study area and species

The study was conducted in La Sauceda forest (530 m above sea level, 36º31´54´´ N, 5º34´29´´ W) in Los Alcornocales Natural Park, a mixed mountain oak woodland of ~ 1700 km^2 in the south of the Iberian Peninsula. The dominant bedrock is Oligo-Miocenic sandstone, giving rise to acidic and sandy soils, with small inclusions of loam and clay soils. The climate is subhumid Mediterranean, with mild temperatures (annual mean of 17 ºC) and frequent mists year-round, due to the proximate confluence of the Mediterranean Sea and the Atlantic Ocean. Annual mean rainfall varies from 900 to 1800 mm, with the heaviest rainfall in autumn, winter and spring, followed by dry summers (see average 1985-2004 data from La Sauceda meteorological station in Fig. 5.1). Forests are co-dominated by evergreen oak *Q. suber* and winter-deciduous *Q. canariensis*, which is more abundant in stands located near streams (Urbieta *et al*. in press, chapter 3); while deciduous *Q. pyrenaica* occurs in small stands at the highest altitudes. See Quilchano *et al*. (2008) for a description of the experimental forest site.

Experimental design and data collection

To encompass intra-specific variation, we collected acorns from several trees (at least ten of each oak species) during the fruiting season (October-December 2003). Acorns of these species are mainly dispersed by gravity, but a significant proportion is dispersed by birds, rodents, or insects, and then buried (Pérez-Ramos *et al*. 2007). Acorns of *Q. suber* and *Q. canariensis* were collected from local stands near the experimental plot, while acorns of *Q. pyrenaica* (with scarce reproduction in the area) were brought from Sierra Morena stands (inland area also in S Spain). Acorns infected by moths or beetle larvae were culled through flotation. Selected acorns were stored on a moist vermiculite bed in plastic trays at 2-4 ºC until used in the experiment; they were individually weighed to the nearest 0.01 g. Mean ± standard deviation (SD) acorn fresh weight (g) was: 4.36 ± 1.63 for *Q. suber*, 4.48 ± 1.38 for *Q. canariensis* and 5.56 ± 1.04 for *Q. pyrenaica*. We used acorn fresh weight as a surrogate of seed mass, justified by their high correlation (Quero *et al*. 2007). Acorns were buried 2-3 cm into the soil and distributed haphazardly across 60 experimental units (minimum distance of 10 meters between units), which spanned a wide and continuous gradient of water and light availability, from open habitats (up to 90 % full sun), to deeper shade under shrubs and trees (down to 5 %). Experimental units were separated from each other at least by 10 m. Each unit consisted of 4 wire cages (25 x 25 x 25 cm, 1.3 cm mesh size) to avoid attack by predators (n=240 cages). Ten acorns of *Q. suber*, 10 acorns of *Q. canariensis*, and 8 acorns of *Q. pyrenaica* were sowed at each unit (5 acorns of either *Q. canariensis* or *Q. suber*, and 2 of *Q. pyrenaica* inside each cage). A total of 600 seeds each of *Q. suber* and *Q. canariensis* were sown on 23 December 2003 and 480 seeds of *Q. pyrenaica*

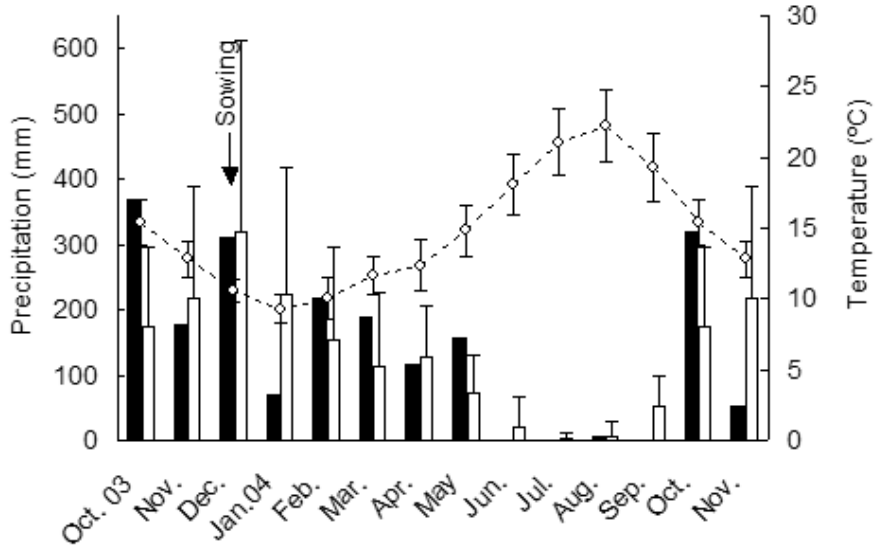

Figure 5.1 Climate diagram for the study area (data from La Sauceda meteorological station). Monthly precipitation values registered during the experiment, from autumn 2003 to winter 2004 (black bars), are compared to the monthly mean ± SD registered from 1985-2004 (white bars). Monthly temperature is represented by the mean ± SD of the values for the period 1985-1997 (dashed line).

were sown on 5 February 2004 when they became available.

Experimental units were censused regularly for one year. We tracked seedling emergence above ground through bi-weekly monitoring. Survival of seedlings and cause of mortality were monitored bi-weekly through spring-autumn (until October 2004) with an additional census in February 2005 (one year after emergence). We considered seedlings to be dead if they lacked green leaves and had brittle stems. In some cases, apparently dead seedlings (by shoot dieback) recovered and resprouted after the summer; these seedlings were re-categorised as live. Germination was assessed indirectly. After the summer, we unearthed acorns from cages without emerged seedlings, and inspected the seeds for radicles (indicating germination). Thus, we were able to estimate germination probability (those emerged plus those non-emerged but germinated / total seeds sown). The very few unearthed acorns (38 in total) that had signs of predation by rodents, beetles or insect larvae were excluded from the analyses.

We estimated species responsiveness to episodic summer rains by watering half of the seedlings (two of the four cages per unit). During three summer months (July-September) we added two litres of water per cage (equivalent to ~ 33 mm rainfall) bi-weekly. Percent soil volumetric water content (SVWC) was measured at each experimental unit (four readings, one per cage, total of 240), using Time Domain Reflectometry (TDR) (Campbell Scientific, Inc., Logan, Utah, USA) with stainless steel rods inserted 12 cm into the soil. Measurements were taken in winter (29 January and 4 March 2004), early spring (2 April) and summer (4 August), in order to characterize soil moisture during wet-dry periods. We calculated minimum, maximum and mean SVWC values, as well as the mean value of the wet period (winter and spring), and oscillation range (difference

between the means of the wet period and summer). We also recorded visual evidence of soil waterlogging (i.e., standing pools of water) in the experimental units during bi-weekly monitoring. Light availability at the seedling level was measured at each of the 60 experimental units with hemispherical canopy photographs (two per experimental unit), using a Nikon Coolpix 4500 camera with fish-eye lens (F8 Nikon), and then analyzing the images with Hemiview Canopy Analysis software (Delta-T Devices Ltd. 1999, v. 2.1). All photographs were taken in October 2004, before *Q. canariensis* trees began to drop their leaves. We selected Global Site Factor (GSF), given in units of percent full sun, as an estimate of understorey light availability. Soil compaction (expressed in MPa) was measured with a penetrometer (Penetrologger, Eijkelkamp Agriserch Equipment, Giesbeek, The Netherlands) in early spring (March 2005). Two measurements were taken per experimental unit in order to characterize the soil profile to 60 cm depth, which could influence seedling rooting, through aeration or mechanical limitation. We calculated minimum, maximum and mean compaction along the profile, as well as compaction of the first 20 cm and at maximum depth (60 cm); we recorded maximum soil depth when reaching bedrock.

Statistical analysis

Each recruitment stage (seed germination, seedling emergence, and survival) was modelled independently as functions of abiotic factors, seed mass and emergence time. In this demographic sequence, germination was analysed for all sowed acorns excluding those that germinated during storage (N=526 for *Q. suber*, N=552 for *Q. canariensis*, N=462 for *Q. pyrenaica*); seedling emergence was analysed for all germinated acorns (N=414 for *Q. suber*, N=288 for *Q. canariensis*, N=337 for *Q. pyrenaica*); and seedling survival for all the emerged seedlings (N=303 for *Q. suber*, N=220 for *Q. canariensis*, N=205 for *Q. pyrenaica*). Values of soil water and light level measured at the cage level were assigned to each acorn / seedling.

Seed germination and seedling emergence models

With maximum likelihood techniques we fitted linear and non-linear models of germination and emergence for each species. These processes can be described by a binomial distribution with likelihood function:

[1] $$L = \prod_{i=1}^{N-D} p_i \prod_{i=1}^{D} (1 - p_i)$$

where, N is the number of individuals starting each stage, D is the number of seeds failing (non germinating or non emerging), and p_i is the probability of germination or emergence for the individual i.

For each species, we specified germination and emergence probabilities (p_i), as functions of abiotic factors: light, soil water content, and soil compaction. In addition, seed mass was tested as a covariate in all models. Different functional responses that covered a wide range of possible forms were fitted: linear, exponential, logistic, Michaelis-Menten-type and power functions (see Appendix 5.1 for equations). We first tested models for each factor and functional response independently. Then, we tested for two factor models using the factors and functional responses that yielded the best fit when evaluated singly.

In addition, we fitted regression models to test how abiotic factors affected emergence times. Based on exploratory analyses of potential distributions that best fitted our data, a gamma distribution of emergence times was assumed. This distribution has a flexible shape defined by a shape parameter (n), which varies from exponential-like to bell-shaped but left-skewed probability distributions (Evans *et al*. 2000). We specified the mean of the gamma distribution as a function of abiotic factors and seed mass using the above-mentioned functional responses, i.e. linear, exponential, logistic, Michaelis-Menten and power, and fitting one and two factor models.

Seedling survival models

Survival analysis and maximum likelihood methods were combined to parameterise survival models as a function of resources (according to Kobe *et al*. 2002). Analogous to the distribution function for a binomial random variable, the likelihood function for a continuous distribution of survival times is:

$$[2] \qquad L = \prod_{i=1}^{D} f(t_i;\phi) \prod_{i=1}^{N-D} S(c_i;\phi)$$

where, the contribution to the likelihood of a seedling observed to die at time *t* is $f(t_i;\phi)$ (i.e., the density of failure at time *t*), and the contribution to the likelihood of an individual surviving beyond time *c* is $S(c_i;\phi)$ (i.e., the survivor function), ϕ is a vector of parameters, *D* represents the number of individuals dying, and *N-D* is the number of individuals surviving beyond time *c*, both indexed by *i* to represent individual seedlings (Cox and Oakes 1984).

We examined survival time distributions of seedlings, and generally the exponential provided the best fits from among the distributions tested (e.g., the exponential resulted in a maximum loglikelihood that was ~ 7 loglikelihood units higher than the normal distribution for *Q. suber*). Although mortality often decreases as seedlings age and grow larger, during this study's focus on first-year seedling establishment, mortality risk was relatively constant (an assumption of the exponential distribution), especially after accounting for environmental influences on mortality (see below). Using an exponential distribution of survival times, the likelihood becomes:

$$[3] \quad L = \prod_{i=1}^{D} M(x_i,\phi) e^{-t_i M(x_i,\phi)} \prod_{i=1}^{N-D} e^{-c_i M(x_i,\phi)}$$

where, $M(x_i, \phi)$ or the hazard function is composed of a vector of explanatory variables x_i and set of parameters ϕ.

We specified the hazard, $M(x_i, \phi)$, as a function of abiotic factors (light, soil water content, and soil compaction), and we also explored the effects of seed mass and emergence times. The same procedure as for germination and emergence was followed, fitting several functional responses (i.e., linear, exponential, logistic, Michaelis-Menten and power), and testing single-factor and two-factor models. The effects of the summer watering treatment on seedling survival was tested by first using the complete data set to identify the factors that were best predictors, and secondly by comparing a general model fit to all the data (without respect to the watering treatment), versus models that were specific to the watering treatment.

Model selection and goodness of fit

Models were parameterised with maximum likelihood (Edwards 1992), using a simulating annealing algorithm (Metropolis *et al*. 1953). To test for the influence of predictors in each regeneration stage, fitted models were compared to a null model of no factor effect using Likelihood Ratio Tests (LRTs) (Edwards 1992). We estimated 95% support regions (equivalent to 95% confidence intervals but used in conjunction with likelihood methods) by likelihood profile (Hilborn and Mangel 1997). All the models and numerical algorithms were implemented in programs we wrote in C (Borland International Inc. 1996, v.5.01). Fitted models were compared with Akaike's Information Criteria, specifically Δ AIC, which is defined for each Model_i as: AIC_i - $\text{AIC}_{\text{minimum}}$ (Akaike 1992). The model with the strongest empirical support has the minimum AIC and thus its Δ AIC= 0. Models with Δ AIC between 0-2 were considered to have equivalent and substantial empirical support, Δ AIC between 4-7 indicated less support and models with Δ AIC >10 were dismissed as they had negligible empirical support (Burnham and Anderson 2002).

Results

Soil water content in winter and spring was very high and spatially heterogeneous, with waterlogging in some experimental units (Mean ± SD SVWC (%) was 46.8 ± 18 in January, 45.3 ± 20 in March, and 53.7 ± 22 in April). However, very dry and homogeneous water conditions were found in summer (9.3 ± 3 % SVWC in August). GSF was positively correlated with mean wet-period SVWC ($r = 0.33$, $p < 0.05$), as well as with the SVWC oscillation between winter and summer ($r = 0.35$, $p < 0.05$). Thus, open areas tended to suffer more winter waterlogging, but dried out in summer reaching similar minimum SVWC values as more shaded areas.

The three oak species diverged substantially in each of the studied recruitment stages: *Q. canariensis* had the lowest seed germination rate (47%), compared to *Q. suber* (71%) and *Q. pyrenaica* (75%). On the contrary, *Q. pyrenaica* had a lower percentage of emerged seedlings above ground (61%) than *Q. suber* (74%) and *Q. canariensis* (76%). *Q. suber* seedlings had lower survival (37%) than *Q. canariensis* (47%) and *Q. pyrenaica* (44%) one year after emergence. Seedling mortality of all the species was mainly due to desiccation and started with warm and dry conditions (late May- early June, Fig. 5.1), until the first autumn rains (October). Shoot dieback was frequent in *Q. pyrenaica* seedlings (61%), recovering in autumn after losing all the leaves in summer, but less frequent (about 12%) in the other two species. Seedling mortality during the subsequent cool and wet period (October-February) was low.

Models were formulated to test alternative hypotheses regarding main factors controlling germination, emergence and seedling survival. Among the tested models, those with the strongest empirical support are described below for each recruitment stage (see Appendixes 5.1 and 5.2 for parameter estimates of all models, and LRTs results).

Seed germination

In all three species, probability of germination declined exponentially with increasing mean SVWC during the wet period, as indicated by the best-supported germination models (Appendix 5.1). Light availability intensified the negative effect of wet-period soil moisture on germination of *Q. suber* and *Q. canariensis*, but light had a small positive effect for *Q. pyrenaica* (Fig. 5.2a). The model including wet-period water and light availability had strong empirical support for *Q. pyrenaica* (Δ AIC= 0) and *Q. canariensis* (Δ AIC= 0.3), and lower support for *Q. suber* (Δ AIC= 5.6) (Appendix 5.1). Species differed in their response to SVWC at any level of the light gradient. Fixing light to its mean value of the gradient (i.e., GSF= 50%), species response to SVWC showed a similar trend (slope), but *Q. canariensis* had lower germination probability than the other two species along the gradient (Fig. 5.2b). We also tested for the effects of light over a narrower range of conditions (5-30 % full sun) to control for possible confounding effects with waterlogging. However, estimated models still showed negative light effects for *Q. suber* and *Q. canariensis*.

For *Q. suber*, in addition to the negative effects of wet-period SVWC, seed mass had positive effects on germination (Fig. 5.2c), as indicated by the model with the greatest empirical support (Appendix 5.1). Other factors such as soil depth and compaction had an effect on species germination but with considerably less empirical support (Appendix 5.1).

Seedling emergence

For all three species, probability of emergence also declined exponentially with wet-period SVWC, as indicated by the models with the strongest empirical support (Appendix 5.1). Models including SVWC of the wet period alone showed the greatest empirical support (Δ AIC= 0) for *Q. suber* and *Q. pyrenaica*, but for both species, models that included seed mass or light availability also had substantial support

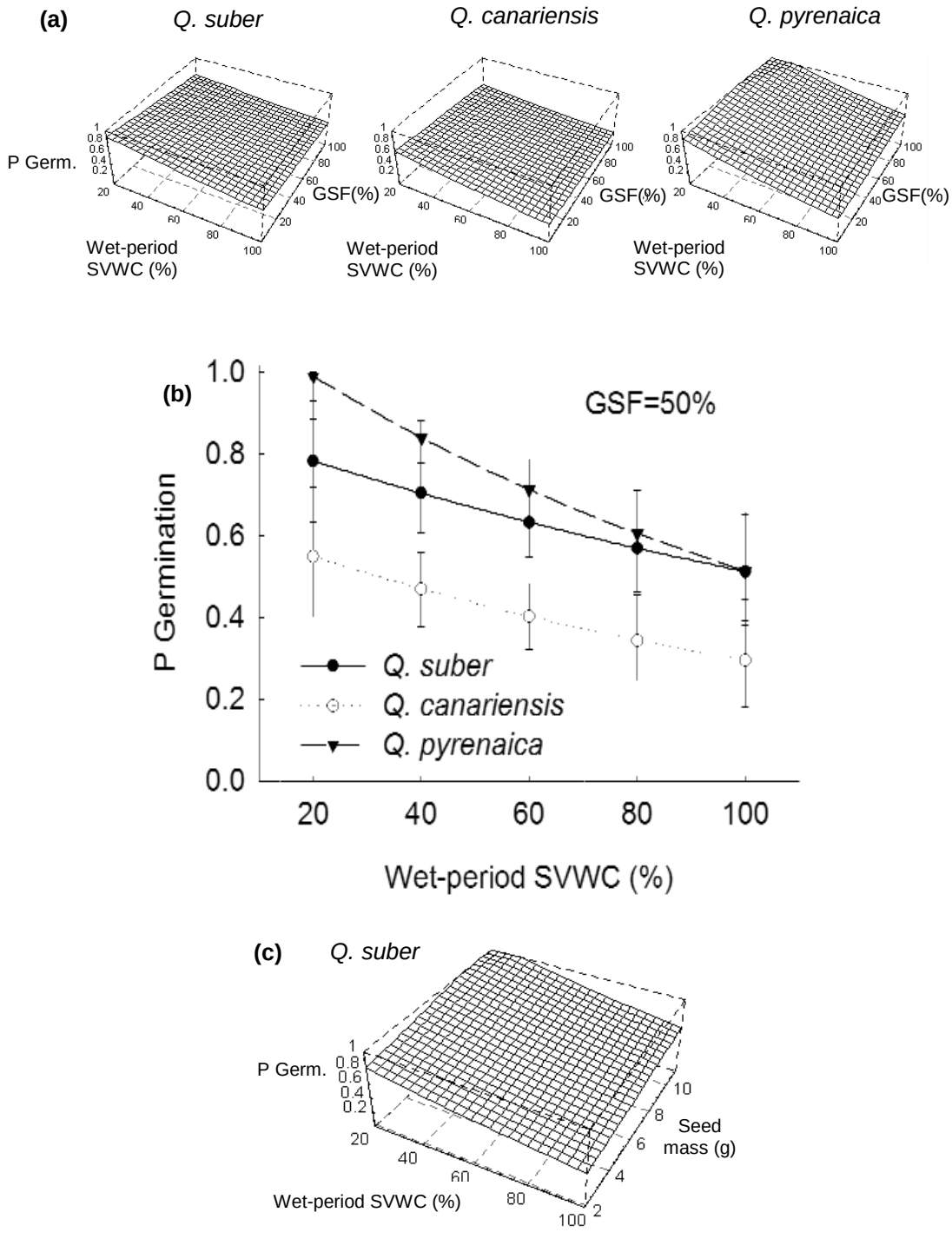

Figure 5.2 (a) Probability of germination of the three oaks exponentially diminished as soil volumetric water content (SVWC) of the wet period increased and light availability (GSF) increased (except for *Q. pyrenaica*). (b) Interspecific differences in responses to wet-period SVWC for a given point of the light gradient (GSF= 50 %). Bars denote 95% support regions. (c) Germination probability of *Q. suber* as function of wet-period SVWC and seed mass.

(within two AIC units of the best supported model). For *Q. canariensis*, emergence probability declined with increases in both wet-period SVWC and seed mass and no other models were within 2 AIC units. Thus, common among all three species, models that included SVWC of the wet period and seed mass had strong empirical support. However, in contrast to *Q. canariensis*, larger seeds of *Q. suber* and *Q. pyrenaica* had higher probability of emergence (Fig. 5.3a). Species differed in their response to SVWC. For a mean value of seed mass (i.e., 5g), probability of emergence diminished as SVWC increased, especially for *Q. pyrenaica* seedlings (Fig. 5.3b). SVWC and light (GSF) equivalently explained emergence of *Q. suber* and *Q. pyrenaica*. A simultaneous increase of soil water content and light availability diminished the emergence probability of *Q. suber* and *Q. canariensis*, while a small positive effect of light was found for *Q. pyrenaica*'s emergence. When examining factor effects over a curtailed light gradient (5-30 % full sun) that excluded the more open waterlogged sites, models including light still showed negative effects on seedling emergence for *Q. suber* and *Q. canariensis*.

Seedling survival

Time to emergence, i.e. number of days elapsed from sowing until seedlings emerged above ground, was the best predictor of seedling survival for all three species (Appendix 5.1). Individuals that emerged earlier had a higher probability of survival during the drought period (Fig. 5.4). Water addition during the dry summer did not improve seedling survival of *Q. suber* (Fig. 5.4a), but did reduce mortality of the two deciduous species. The beneficial effect of summer watering was stronger for *Q. canariensis* seedlings that emerged earlier, i.e., watered and non-watered curves converged for late emergence (Fig. 5.4b). *Q. pyrenaica* watered seedlings showed a similar probability of survival (but always greater than non-watered individuals) whenever they emerged (Fig. 5.4c). Parameter 95% support regions of the three oaks overlapped for non-watered individuals (figure not shown); thus, there was no strong difference among species in their survival responses to emergence times under field conditions.

Emergence time

Because seedling survival during the dry period was best predicted by emergence time, we also analysed how abiotic factors and seed mass affected species emergence times. In general, emergence times followed a decreasing distribution, with a greater number of seedlings emerging in March-April (70-80 days after sowing) and reaching lower percentages as summer approached. The start of emergence was earlier for *Q. canariensis* and *Q. pyrenaica* (40 days after sowing) than for *Q. suber* (70 days), and the total emergence length was shorter for *Q. pyrenaica* (up to 140 days) than for the other two species (up to 195 days). Mean soil moisture (SVWC) during the wet period was the key factor influencing species emergence time, as indicated by the models with the strongest empirical support (Appendix 5.2), with higher SVWC associated with later emergence times. In addition, variability among individual emergence times was higher in the wettest soils. Seedlings of *Q. suber* needed, on average, a longer time to emerge compared to the other species at any level of the water gradient. For all three species, additional factors influenced emergence time, as indicated by the best-supported models (Appendix 5.2). Wet-period SVWC and seed mass explained emergence timing of *Q. pyrenaica*, with larger seeds associated with a more delayed emergence. For *Q. suber* and *Q. canariensis*, light availability intensified the effect of wet-period soil moisture on delaying seedling emergence.

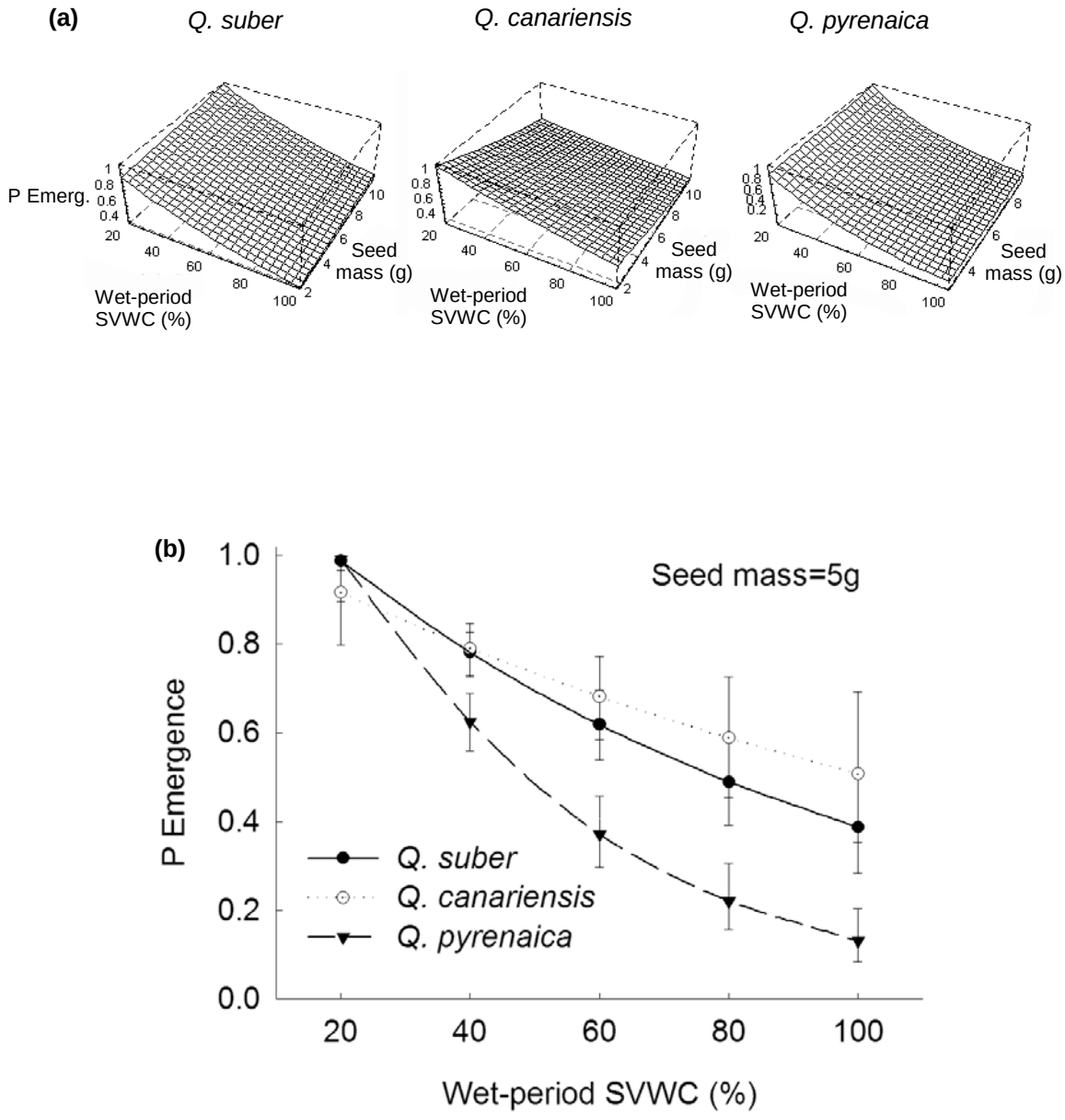

Figure 5.3 (a) Probability of emergence of the three oaks exponentially diminished as wet-period soil volumetric water content (SVWC) increased and seed mass decreased (except for *Q. canariensis*). Notice different scales in the axes. (b) Interspecific differences in responses to wet-period SVWC for an average seed mass of 5 g. Bars denote 95% support regions.

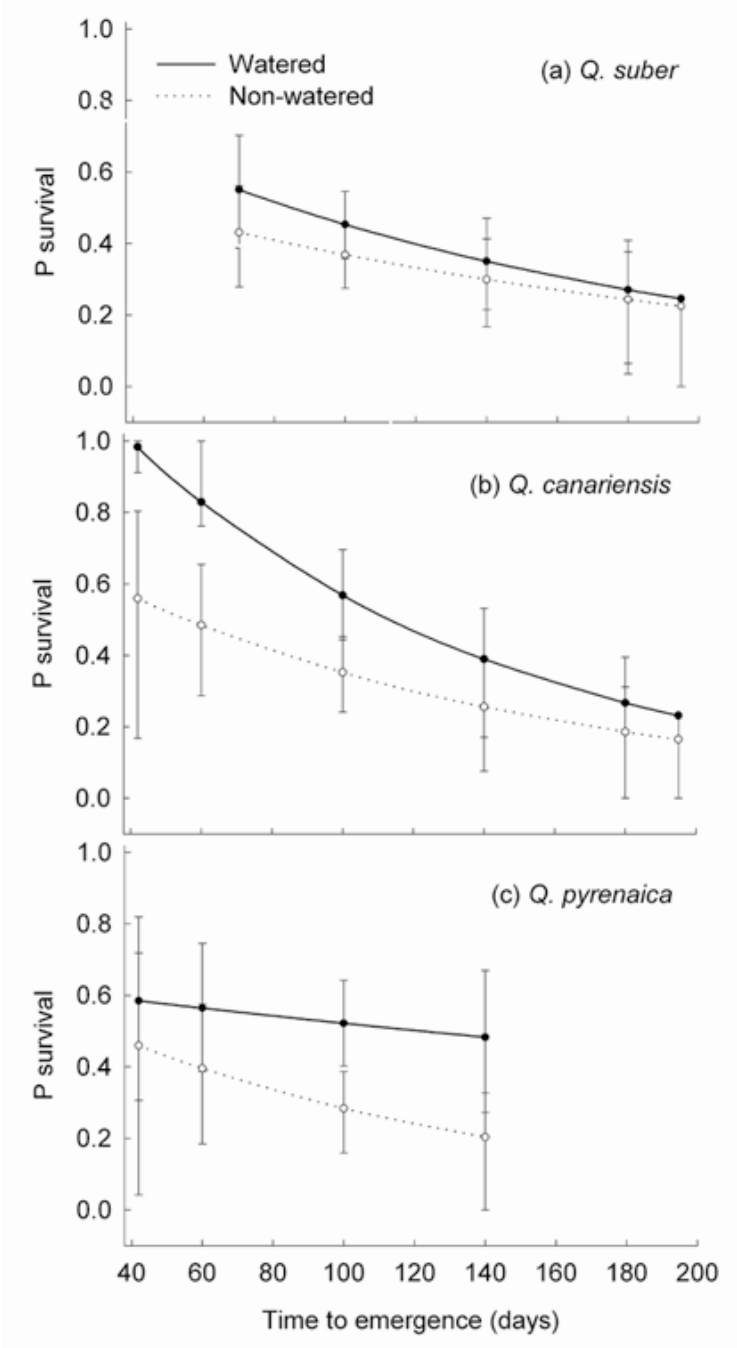

Figure 5.4 Models resulting from the best fit for seedling survival. Responses of watered and non-watered (control) individuals are differentiated. Probability of survival in summer was lower for those seedlings that delayed their emergence. *Q. suber* seedlings did not respond to the water treatment (a). Watering significantly increased *Q. canariensis*' (b) and *Q. pyrenaica*'s (c) survival.

Discussion

Resource availability and oak establishment

Spatial and temporal soil water heterogeneity (from waterlogged to very dry conditions) was the major factor controlling, either directly or indirectly through emergence time, seedling establishment in the studied sub-humid Mediterranean forest. Drought (i.e., soil water deficit) primarily limiting seedling establishment has been commonly reported by previous studies in the Mediterranean (Rey Benayas 1998; Gómez-Aparicio *et al*. 2005); however, here we found evidence of two seasonal, water-related constraints primarily affecting seedling establishment: water excess in the wet period and water shortage during the dry summer. The stress caused by over-abundant water during the wet season greatly limited seedling establishment through reducing germination and emergence. Moreover, high soil water levels lengthened time to emergence of seedlings, which in turn decreased their survivorship during summer drought (Fig. 5.5). The importance of this factor (local waterlogging) for tree regeneration has been mostly overlooked under Mediterranean conditions.

Some recruitment stages were influenced by the combined effect of both soil water and light. In general, a negative effect of light availability was found for most of the stages (i.e., lower probability of germination and emergence in more open areas). This effect partly arose from the positive correlation between GSF and wet-period SVWC, which indicates that relatively open areas tended to suffer more waterlogging due to higher soil water retention and the absence of rainfall interception by vegetation. However, the negative effect of irradiance was still present even when looking at a curtailed range of light conditions. In the mosaic of soils found in the studied forests, more clayey patches have poorer drainage, leading to conditions less suited for the colonization and establishment of woody species. These conditions are reflected in sparse woody vegetation and higher light availability. Winter waterlogging was associated with the presence of low permeability clayey soils, which show strong redoximorphic features in the profile (L.V. García, pers. com.) that are indicative of seasonal soil saturation (Jacobs *et al*. 2002). We hypothesise that seedlings may have experienced low oxygen concentration (hypoxy) while in seasonally waterlogged soil, potentially curtailing respiration and impeding radicle and shoot development (e.g., Schmull and Thomas 2000). In a parallel study, submerging acorns of these three oak species for prolonged periods (> 30 days) in controlled conditions (to prevent fungal infection) resulted in reduced and delayed germination and hampered root development (Pérez-Ramos 2007). Similar negative effects of clayey hydromorphic soils, which suffer temporal waterlogging and sporadic dry periods, have been found in declining stands of Atlantic temperate oak forests (Thomas and Hartmann 1998; Vincke and Delvaux 2005).

Our results suggest that water can act as a double factor of stress (by excess and deficit), rather than as a resource, during the initial stages of seedling recruitment in forest ecosystems with contrasting seasonal rainfall regimes. Nevertheless, other factors not recorded here - soil nutrients or herbivory - might also influence the multidimensional regeneration niche (Canham *et al*. 1996) of these oak species.

Effects of seed size and emergence time on seedling establishment

We confirmed that initial seed mass and emergence timing mediated the response of seedlings to waterlogging and light availability. For germination of *Q. suber* and emergence of all three oak species, models that included soil conditions (water content) and seed mass provided best fits. This might be due to the important role played by seed reserves in large-seeded species such as oaks during early development (Bonfil 1998; Quero *et al*. 2007), principally under resource stress (Moles and

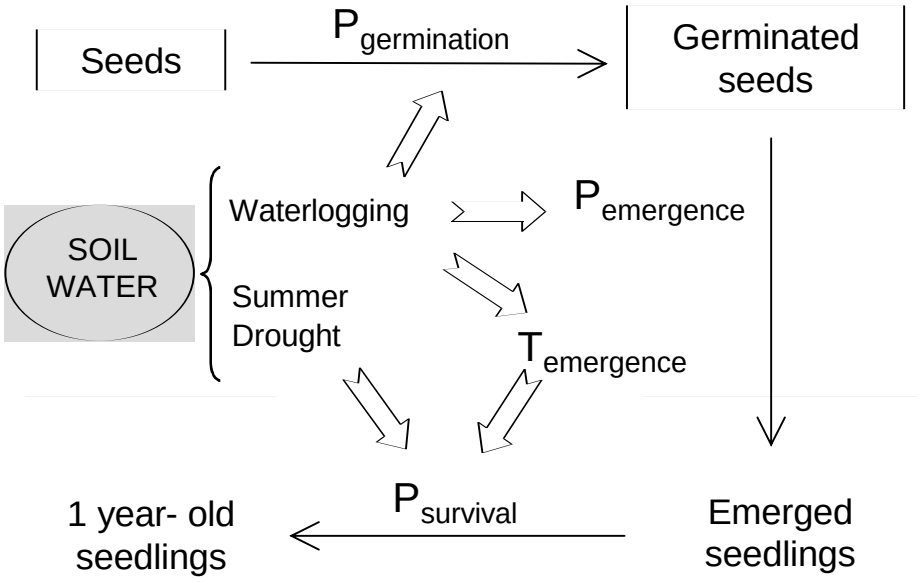

Figure 5.5 Diagram of oak's regeneration cycle with the main factors controlling each of the studied stages. High levels of soil water content (waterlogging) registered during the wet period (autumn to spring) reduced species germination and emergence. Moreover, seedling survival was indirectly (through emergence time) affected by soil water excess, which delayed seedling emergence and shorted the time window of the growing season. Seedlings with delayed emergence had a higher probability of mortality during the summer drought.

Westoby 2004). Within the same oak species, seedlings with larger seeds showed in general higher probabilities of germination and emergence, with the exception of those of *Q. canariensis*, which would merit further study. Positive effects of seed size were more apparent in non-waterlogged microsites. In a parallel study, larger seeds experienced a higher probability of removal by rodents (see chapter 4), which may have been predated or dispersed. Similarly, Gómez (2004) found conflicting selective pressures between a positive effect of (*Q. ilex*) acorn size on most fitness components related to seedling establishment, and direct negative effect of acorn size on survival to predation.

Early seedling emergence had a strong positive effect on survival for all three oak species. Differences among emergence dates may be controlled either by phenotypic and genetic effects related to seeds, or by environmental conditions experienced by the germinating seed (Jones *et al*. 1997). In this study, those seedlings that did not suffer waterlogging emerged earlier and could benefit from growing season (spring) resources for a longer period of time. Thus, intra-specific differences in emergence times were primarily due to differences in environmental conditions of the germinating seed. Similarly, Castro (2006) found that emergence time determined establishment success (higher probability of survival and growth) of *Pinus sylvestris* seedlings in SE Spain, across microhabitats, and irrespective of the intensity of summer drought. In Mediterranean plant communities, seedling survival of different species during the dry period is positively correlated with root allocation (Lloret *et al*. 1999). Thus,

with a better phenological match to resource availability and avoidance of waterlogging, seedlings that emerged earlier likely developed root systems more fully, which enabled greater survival during the dry period (Nicotra *et al*. 2002).

Oak regeneration ecology and forest dynamics

Identification of seedling functional responses along resource gradients is critical to achieve a mechanistic understanding of vegetation dynamics (Pacala *et al*. 1996; Kobe 1999). In the present study, the same functional responses and factors (mainly soil water during the wet period) characterized the responses of three oaks, but mortality peaks occurred in different life stages for different species. *Q. canariensis* had the lowest germination rate among species. However, germinated acorns of *Q. canariensis* succeeded most in emergence and survival (especially if they could emerge early and were watered in summer). On the contrary, *Q. pyrenaica* showed the highest probability of germination, whatever the soil water level, but waterlogging sharply reduced probability of emergence. *Q. pyrenaica*'s emergence times (despite their delayed planting) were similar to those of *Q. canariensis*. Seedlings of both deciduous species responded positively to water addition during the dry period, supporting previous studies showing the benefits of summer rains on seedling survival (Castro *et al*. 2005) and growth (Castro-Díez *et al*. 2006). *Q. suber* had an intermediate response in germination (equivalent to *Q. pyrenaica*) and emergence (similar to *Q. canariensis*), but suffered higher mortality in summer, primarily because seedlings emerged later and experienced a shorter time window between when soils were too wet and when they were too dry. In addition, evergreen *Q. suber* had a weak response to water addition during the summer, which is consistent with a greenhouse study where watering increased stomatal conductance, photosynthesis and respiration in deciduous *Q. pyrenaica* and *Q. canariensis*, but not in *Q. suber* (Quero *et al*. 2006).

The intensity and timing of rainfall, and hence variation in soil water content, may be critical in driving forest structure and dynamics. Seasonal water heterogeneity (with waterlogging and drought events) captured during the experiment typified long term climatic data for the study region (see Fig. 5.1). Consequently, in most years, tree seedlings suffer an excess-deficit water cycle, in which emergence time must be critically balanced between avoiding waterlogging and being large enough to resist drought, in order to establish. Inter-annual climatic variation can alter the quality of microhabitats for seedling establishment in heterogeneous Mediterranean forests (Gómez-Aparicio *et al*. 2005). Thus, between-year variation in precipitation (i.e., drier winters or sporadic rains in summer) and differences in rainfall timing (i.e., early versus late), could differentially impact species establishment patterns.

Our modelling approach can help elucidate how oak establishment might change spatially and across years, because species-specific responses were parameterised across broad light and water gradients. Although we must be cautious in extrapolating a one year study to longer time scales, we speculate that under a drier winter (without waterlogging) *Q. suber* would benefit disproportionately among these species, since it had higher germination and emergence rates at the driest part of the water gradient. Conversely, *Q. suber* would be negatively affected by wet winter conditions and late rains due to its later seed drop compared to *Q. canariensis* (Pérez-Ramos 2007), and its greater delay in emergence under waterlogged conditions, which would then shorten its time window for growing before the summer. We also speculate that sporadic summer rain events would provide greater benefit to deciduous species (especially *Q. canariensis*), because their survival improved when watered in summer, and thus, they could gain an advantage over *Q. suber* in nutrient-rich and more mesic habitats. These qualitative predictions are consistent with the species landscape distributions, *Q. canariensis*

being more abundant near stream beds, while *Q. suber* under drier conditions (Urbieta *et al*. in press; chapter 3).

We hypothesise that if autumn-spring rainfall regimes persist (with waterlogging) but the onset of summer drought advances, there may no longer be an adequate time window for oak seedlings to develop the root systems necessary to tolerate summer drought, thereby intensifying problems with oak regeneration. On the other hand, decreased rainfall during the wet period could alleviate waterlogging in clayey soils, promoting seedling establishment in areas that currently do not support woody vegetation. The sensitivity of early seedling life history stages to soil water suggests that changes in the precipitation regime or temperature-mediated effects on water balance could have major impacts on regeneration dynamics in Mediterranean oak forests.

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Appendix 5.1

Table 5.1 Maximum likelihood parameter estimates for germination, emergence and survival models. Models are ranked from best to poorest fits.

GERMINATION

	Factor 1	Factor 2	Fit	A	S	D	LogLike.	LRT ($\times^2$)	AIC	ΔAIC
Q. suber	Wet-period SVWC (%)	Seed mass (g)	EXP+	0.86	-0.0069	0.0340	-301.1	28.5***	608.2	**0.0**
	Max. SVWC (%)		EXP	0.99	-0.0059		-304.4	21.9 ***	612.8	4.6
	Wet-period SVWC (%)	GSF (%)	EXP+	1.00	-0.0053	-0.0028	-303.9	22.9***	613.8	5.6
	Wet-period SVWC (%)	GSF (%)	EXP*	0.83	0.0000	-2.5642	-304.3	22.4***	614.6	6.5
	Wet-period SVWC (%)		EXP	0.98	-0.0068		-305.4	19.9 ***	614.8	6.6
	GSF (%)		EXP	0.83	-0.0048		-308.6	13.3 ***	621.3	13.1
	Seed weight (g)		EXP	0.59	0.0454		-311.7	7.3 **	627.4	19.2
	Max. depth (cm)		LIN	0.57	0.0040		-312.6	5.4 *	629.3	21.1
	Null model			0.71			-315.3		632.7	24.5
	Factor 1	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**ΔAIC**
Q. canariensis	Wet-period SVWC (%)		EXP	0.73	-0.0093		-375.4	13.0***	754.8	**0.0**
	Wet-period SVWC (%)	GSF (%)	EXP+	0.74	-0.0078	-0.0029	-374.5	14.7***	755.1	**0.3**
	Wet-period SVWC (%)	GSF (%)	EXP*	0.57	-0.0386	0.0033	-374.6	14.6***	755.2	**0.4**
	Wet-period SVWC (%)	Seed mass (g)	EXP+	0.75	-0.0092	-0.0068	-375.4	13.1**	756.8	**1.9**
	Max. SVWC (%)		EXP	0.68	-0.0067		-376.6	10.7**	757.1	2.3
	GSF (%)		EXP	0.56	-0.0054		-378.5	6.7 **	761.0	6.2
	Mean compact. (MPa)		MM	0.68	0.7574		-379.4	5.0 *	762.8	8.0
	Max. compact. (MPa)		MM	0.59	0.6000		-379.8	4.2 *	763.6	8.8
	Null model			0.47			-381.9		765.8	11.0
	Factor 1	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**ΔAIC**
Q. pyrenaica	Wet-period SVWC (%)	GSF (%)	EXP+	1.00	-0.0081	0.0029	-239.4	37.4***	484.8	**0.0**
	Wet-period SVWC (%)		EXP	1.10	-0.0081		-244.4	27.5 ***	492.7	7.9
	Max. SVWC (%)		EXP	1.07	-0.0063		-245.2	25.8 ***	494.4	9.6
	Wet-period SVWC (%)	Seed mass (g)	EXP+	1.13	-0.0081	-0.0041	-244.4	27.5***	494.7	9.9
	Superf. compact. (MPa)		MM	0.95	2.1390		-253.6	9.0 **	511.2	26.4
	Mean compact. (MPa)		MM	0.91	2.1220		-255.2	5.8 *	514.5	29.6
	GSF (%)		LIN	0.70	0.0018		-256.2	3.8 *	516.4	31.6
	Null model			0.75			-258.1		518.3	33.5

Table 5.1 Continued

EMERGENCE									
Factor 1	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**ΔAIC**
Wet-period SVWC (%)		EXP	1.25	-0.0117		-213.4	46.4 ***	430.7	**0.0**
Wet-period SVWC (%)	Seed mass (g)	EXP+	1.16	-0.0116	0.0150	-212.7	47.6***	431.0	**0.3**
Wet-period SVWC (%)	GSF (%)	EXP+	1.25	-0.0106	-0.0018	-212.6	47.8***	431.3	**0.6**
Max. SVWC (%)		LIN	1.09	-0.0065		-214.1	44.8 ***	432.3	**1.6**
Wet-period SVWC (%)	GSF (%)	EXP*	0.91	0.0034	-0.0462	-218.5	36.1***	443.0	12.3
GSF (%)		EXP	0.89	-0.0064		-228.2	16.7 ***	460.4	29.7
Wet-period SVWC (%)	Seed mass (g)	EXP*	0.97	-0.0508	0.0270	-227.5	18.1***	461.0	30.3
Superf. compact. (MPa)		MM	0.98	1.8178		-232.1	9.0 **	468.1	37.4
Max. compact. (MPa)		LOGI	0.31	0.1643		-233.6	5.9 *	471.2	40.5
Null model			0.74			-236.6		475.1	44.4
Factor 1	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**ΔAIC**
Wet-period SVWC (%)	Seed mass (g)	EXP+	1.39	-0.0070	-0.0627	-146.1	22.7***	298.1	**0.0**
Wet-period SVWC (%)	Seed mass (g)	EXP*	1.10	-0.2595	0.0071	-147.8	19.1***	301.7	3.6
Max. SVWC (%)		EXP	1.05	-0.0060		-150.4	14.0 ***	304.8	6.7
Wet-period SVWC (%)		EXP	1.06	-0.0074		-151.0	12.7 ***	306.1	7.9
Wet-period SVWC (%)	GSF (%)	EXP+	1.08	-0.0068	-0.0014	-150.6	13.7**	307.1	9.0
Wet-period SVWC (%)	GSF (%)	EXP*	0.86	0.3494	-0.0002	-152.4	9.9**	310.8	12.7
Seed mass (g)		EXP	1.02	-0.0660		-154.1	6.6 *	312.2	14.0
GSF (%)		LOGI	1.56	-0.0124		-155.2	4.4 *	314.4	16.2
Null model			0.76			-157.4		316.8	18.7
Factor 1	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**ΔAIC**
Wet-period SVWC (%)		EXP	1.77	-0.0261		-170.0	111.2 ***	344.0	**0.0**
Wet-period SVWC (%)	Seed mass (g)	EXP+	1.52	-0.0250	0.0205	-169.2	112.8***	344.3	**0.3**
Wet-period SVWC (%)	GSF (%)	EXP+	1.74	-0.0267	0.0014	-169.4	112.4***	344.8	**0.7**
Max. SVWC (%)		EXP	1.58	-0.0200		-171.6	108.1 ***	347.1	3.1
Wet-period SVWC (%)	Seed mass (g)	EXP*	1.24	0.0747	-0.0416	-186.2	78.8***	378.4	34.4
Wet-period SVWC (%)	GSF (%)	EXP*	0.84	0.0180	-0.0132	-206.6	38.1***	419.1	75.1
Superf. compact. (MPa)		LIN	0.29	0.1632		-212.0	27.2 ***	428.0	84.0
Mean compact. (MPa)		LIN	0.22	0.1669		-213.3	24.6 ***	430.6	86.5
GSF (%)		EXP	0.71	-0.0052		-222.4	6.5 *	448.7	104.7
Null model			0.61			-225.6		453.2	109.2

Table 5.1 Continued

	SURVIVAL									
	Factor 1	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT (×^{2})**	**AIC**	**Δ AIC**
Q. suber	Time to emergence (days)		LIN	0.02	0.0004		-692.1	20.3***	1388.1	**0.0**
	Oscillation SVWC (%)	Seed mass (g)	LIN+	0.07	0.0008	-0.0065	-694.0	16.4***	1394.0	5.9
	Seed mass (g)		EXP	0.14	-0.1700		-695.5	13.5***	1395.0	6.9
	Oscillation SVWC (%)		LIN	0.04	0.0010		-698.2	8.0**	1400.5	12.4
	Oscillation SVWC (%)	GSF (%)	LIN+	0.04	0.0010	-0.00004	-698.2	8.0*	1402.4	14.3
	Mean SVWC (%)		LIN	0.03	0.0010		-699.3	5.8*	1402.6	14.5
	Null model			0.07			-702.2		1406.4	18.3
Q. can.	**Factor 1**	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT (×^{2})**	**AIC**	**Δ AIC**
	Time to emergence (days)		LIN	-0.002	0.0006		-444.1	24.3***	892.2	**0.0**
	Null model			0.06			-456.2		914.5	22.3
Q. pyrenaica	**Factor 1**	**Factor 2**	**Fit**	**A**	**S**	**D**	**LogLike.**	**LRT (×^{2})**	**AIC**	**Δ AIC**
	Time to emergence (days)		LIN	0.04	0.0003		-415.9	32.1***	835.8	**0.0**
	Oscillation SVWC (%)	GSF (%)	LIN+	-0.02	0.0019	0.0013	-417.2	29.6***	840.3	4.5
	GSF (%)		LIN	0.03	0.0014		-421.1	21.7***	846.2	10.4
	Mean SVWC (%)		LIN	-0.02	0.0030		-423.3	17.3***	850.6	14.8
	Oscillation SVWC (%)		LIN	-0.002	0.0024		-424.5	14.8***	853.1	17.3
	Oscillation SVWC (%)	Seed mass (g)	LIN+	0.01	0.0024	-0.0030	-424.3	15.3***	854.6	18.8
	Min. SVWC (%)		EXP	0.03	0.1004		-428.2	7.6**	860.3	24.5
	Null model			0.06			-431.9		865.9	30.1

Note: Models are noted as LIN (Linear), LOGI (Logistic), MM (Michaelis-Menten), EXP (Exponential), and POW (Power). A and S are parameters estimated in the models (see equations below). D is the estimated parameter when Factor 2 was added to the functional response that yielded the best fit when evaluated singly. Additive interactions between two factors are noted as (+) and multiplicative as (*).
LogLike. corresponds to the maximum log-likelihood: log(Lq|data, model). Factors' effects are evaluated through loglikelihood ratio test (LRT, *p<0.05, **p<0.01, ***p<0.001). AIC (Akaike's Information Criteria) is calculated as: AIC = -2log(Lq|data, model) + 2K, being K the number of parameters in the model. Model fits are evaluated through Δ AIC ($AIC_i - AIC_{min}$). Bold font denotes models with equivalent empirical support (i.e., Δ AIC<2).

Linear: $A + SFactor_i$ Exponential: $Ae^{(SFactor_i)}$ Power: $AFactor_i^S$ Logistic: $\frac{e^{(A+SFactor_i)}}{1+e^{(A+SFactor_i)}}$

Michaelis-Menten: $\frac{AFactor_i}{\frac{A}{S}+Factor_i}$

Appendix 5.2

Table 5.2 Maximum likelihood parameter estimates for best-fitted models that relate emergence time of three oak species with seed mass and abiotic factors. Models are ranked from best to poorest fits.

TIME TO EMERGENCE

	Factor 1	Factor 2	Fit	n	A	S	D	LogLike.	LRT ($\times^2$)	AIC	Δ AIC
Q. suber	Wet-period SVWC (%)	GSF (%)	EXP+	12.0	77.6	0.0055	0.0025	-1463.7	45.6***	2935.4	**0.0**
	Wet-period SVWC (%)		EXP	11.7	79.9	0.0065		-1468.2	36.6***	2942.5	7.1
	Wet-period SVWC (%)	Seed mass (g)	EXP+	11.8	85.1	0.0063	-0.0126	-1467.3	38.4***	2942.6	7.2
	GSF (%)	Seed mass (g)	EXP+	11.2	102.5	0.0038	-0.0161	-1475.1	22.9***	2958.1	22.7
	GSF (%)		EXP	11.2	95.3	0.0038		-1476.4	20.2***	2958.8	23.4
	Null model			10.4	105.7			-1486.5		2977.0	41.6
	Factor 1	**Factor 2**	**Fit**	**n**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**Δ AIC**
Q. canariensis	Wet-period SVWC (%)	GSF (%)	EXP+	12.3	66.7	0.0069	0.0015	-1019.1	42.2***	2046.1	**0.0**
	Wet-period SVWC (%)		EXP	12.2	68.8	0.0071		-1020.2	39.9***	2046.4	**0.3**
	Wet-period SVWC (%)	Seed mass (g)	EXP+	12.1	67.2	0.0071	0.0054	-1020.2	40.0***	2048.3	2.2
	GSF (%)		MM	10.8	106.6	44.5312		-1033.9	12.6***	2073.7	27.6
	GSF (%)	Seed mass (g)	EXP+	10.6	84.3	0.0028	0.0079	-1036.2	7.9**	2080.4	34.3
	Null model			10.2	94.5			-1040.2		2084.3	38.2
	Factor 1	**Factor 2**	**Fit**	**n**	**A**	**S**	**D**	**LogLike.**	**LRT ($\times^2$)**	**AIC**	**Δ AIC**
Q. pyrenaica	Wet-period SVWC (%)	Seed mass (g)	EXP+	12.5	66.6	0.0049	0.0286	-922.8	14.8***	1853.6	**0.0**
	Wet-period SVWC (%)		EXP	12.5	78.0	0.0049		-924.1	12.2**	1854.2	**0.6**
	Wet-period SVWC (%)	GSF (%)	EXP+	12.4	77.9	0.0048	0.0002	-924.1	12.2**	1856.2	2.6
	GSF (%)	Seed mass (g)	EXP+	12.2	75.6	0.0014	0.0316	-926.8	6.8*	1861.7	8.1
	Seed mass (g)		LIN	12.1	77.4	2.9367		-927.9	4.6*	1861.8	8.2
	GSF (%)		EXP	12.1	90.3	0.0013		-928.3	3.9*	1862.6	8.9
	Null model			11.9	93.8			-930.2		1864.4	10.8

Note: Models are noted and evaluated as in Table 5.1. *n* is the shape parameter of the gamma distribution of emergence times, where n>1 indicates bell-shaped but left skewed probability distribution.

Capítulo 6

Capítulo 6

Discusión general: síntesis multiescala

Nuestra habilidad para comprender la estructura y composición de los bosques es clave para lograr una buena gestión, conservación y restauración ecológica de estos ecosistemas. Abordar el análisis de la estructura de las comunidades vegetales a diferentes escalas espaciales permite estudiar las respuestas de los sistemas a los principales factores que operan a través de varias escalas de organización biológica (Wiens 1989; Reed *et al.* 1993). En los capítulos de esta Tesis Doctoral se ha aplicado una aproximación de análisis jerárquico, *hierarchical modelling approach* (ver Willis y Whittaker 2002; Pearson y Dawson 2003), en la que se ha ido modificando la escala espacial de análisis (desde una escala regional, al paisaje, rodal y microhábitat), combinando datos de inventarios forestales, bases de datos cartográficos y resultados de trabajos experimentales. Esta metodología multiescala nos ha permitido identificar diversos factores determinantes de la distribución y estructura de las principales especies forestales del sur de la Península Ibérica, así como analizar sus patrones y procesos de regeneración a lo largo de gradientes ambientales (Fig. 6.1). A continuación, a modo de síntesis vamos a integrar los resultados obtenidos a estas diferentes escalas.

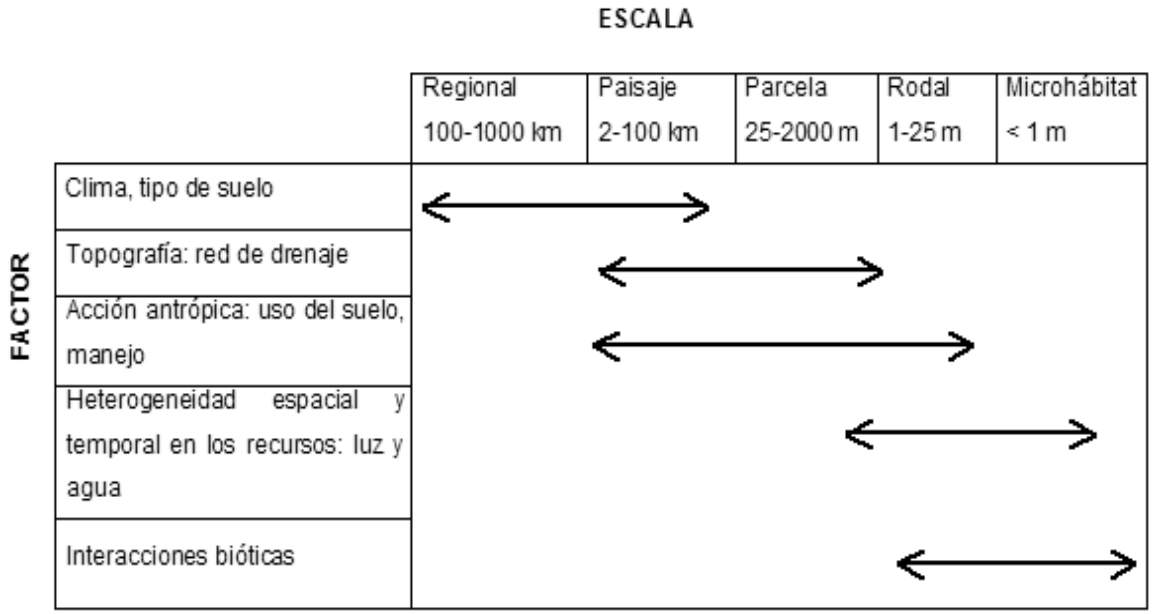

Figura 6.1 Esquema que ilustra cómo diferentes factores (abióticos, bióticos, antrópicos) operan a diferentes escalas espaciales como determinantes de la distribución y estructura de las especies arbóreas mediterráneas estudiadas. Modificado a partir de Willis y Whittaker (2002), Pearson y Dawson (2003).

Estructura de los bosques a lo largo de gradientes ambientales: influencia de los factores abióticos, las interacciones entre especies y la gestión forestal

La distribución de las especies vegetales a gran escala está determinada fundamentalmente por factores de tipo abiótico como el clima (Woodward 1987), pero la presencia de otras especies y sus interacciones pueden influir de forma importante en la abundancia y estructura de las comunidades arbóreas a lo largo de los gradientes ambientales (Callaway y Walker 1997). En el capítulo 2 se ha mostrado que las especies de pinos y robles del sur de la Península Ibérica presentan patrones de segregación a lo largo de gradientes fundamentalmente de tipo climático y edáfico a escala regional, confirmando las evidencias de estudios similares (Rouget *et al.* 2001; Thuiller *et al.* 2003; Purves *et al.* 2007). Los pinos aparecieron asociados al gradiente térmico, mientras que un gradiente de disponibilidad hídrica explicó fundamentalmente la distribución diferencial de los robles. El contenido en calcio del suelo fue un factor clave a la hora de diferenciar la distribución de algunas especies como el pino carrasco (*P. halepensis*), claramente asociado a suelos básicos, mientras que otras especies como el alcornoque (*Q. suber*) y el quejigo moruno (*Q. canariensis*) están asociadas a suelos ácidos.

Al explorar la estructura de los bosques a partir de los datos del Segundo Inventario Forestal Nacional, se detectó una preocupante falta de regeneración forestal, con una proporción de rodales sin regenerado que variaba entre un 20% y un 60% para las especies de *Quercus*, y entre un 40% y un 50% para las especies de *Pinus*. A lo largo de los gradientes ambientales principales se encontró que las curvas de abundancia entre los adultos y el regenerado diferían para algunas especies, lo que pone de manifiesto que los requerimientos ambientales pueden variar a lo largo del ciclo de vida de los individuos, dando lugar a cambios ontogenéticos en sus nichos (Cavender-Bares y Bazzaz 2000; Miriti 2006; Quero *et al.* 2007). Se observó que los pinos regeneraban tanto bajo su propio dosel como de forma importante en zonas forestales sin cobertura arbórea, reflejando su mayor tolerancia a niveles elevados de radiación (Gómez-Aparicio *et al.* 2006), y su capacidad de colonizar nuevos hábitats (Richardson 1998). En algunas especies de *Quercus*, concretamente en la encina (*Q. ilex*) y el quejigo (*Q. faginea*), se observó una mayor abundancia de regeneración en el extremo del gradiente con mayor limitación ambiental, es decir, en las zonas más frías y áridas, donde no se desarrollaban encinares ni quejigares (Fig. 6.2). En estas zonas, donde cabría esperar que las condiciones microclimáticas fueran más limitantes para el establecimiento de plántulas de *Quercus*, la regeneración de encina y de quejigo se daba bajo la copa de los pinares. La cobertura de los pinares probablemente alivia el estrés ambiental, reduciendo la intensidad de la radiación y el déficit de agua, lo que facilita el posterior establecimiento de las plántulas de *Quercus,* que necesitan cierto grado de sombra para establecerse (Espelta *et al.* 1995; Broncano *et al.* 1998). Estudios previos han descrito la capacidad de las especies de *Quercus* para establecerse bajo el dosel de los pinares (Galindo-Jaimes *et al.* 2002; Pausas *et al.* 2006), siendo la dispersión de bellotas por el arrendajo (*Garrulus glandarius*) uno de los posibles mecanismos descritos (Gómez 2003; Pons y Pausas 2007). También es posible que los patrones encontrados sean parcialmente resultado de las reforestaciones de pinos realizadas en hábitats donde previamente se desarrollaban encinares y quejigares (Pausas *et al.* 2004).

Los resultados sugieren que los pinares pueden estar ejerciendo un efecto de facilitación en el establecimiento de las especies de *Quercus*, con el resultado de la expansión de su distribución (o nicho realizado) hacia zonas con condiciones ambientales más extremas (Fig. 6.2). Esto apoya las evidencias empíricas encontradas en ecosistemas mediterráneos donde las interacciones netas positivas, es decir, de facilitación entre especies son más probables a medida que la severidad

ambiental aumenta (Maestre *et al.* 2003; Gómez-Aparicio *et al.* 2004). Por tanto, la distribución y estructura de las masas forestales a escala regional aparecen controladas por la influencia conjunta de los limitantes climáticos y edáficos, así como por las interacciones entre especies.

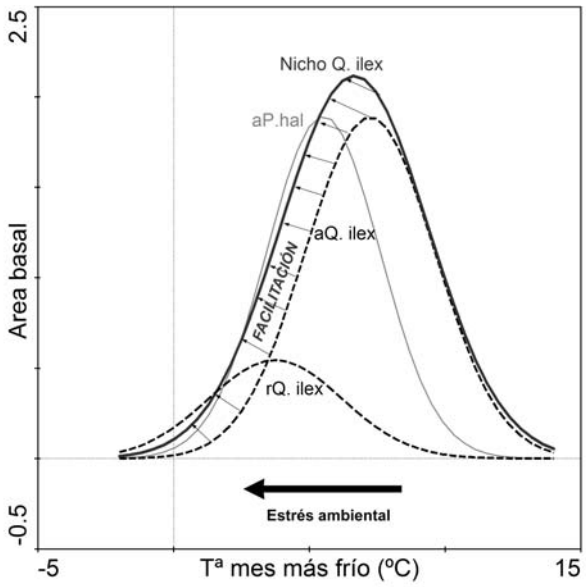

Figura 6.2 Abundancia (área basal, m^2/ha) de la encina (*Quercus ilex*) a lo largo del gradiente de temperatura media del mes más frío (ºC). La curva de regeneración de la encina (rQ.ilex) está desplazada hacia zonas más frías que la curva de abundancia de adultos (aQ.ilex). En este extremo del gradiente la encina regenera bajo el dosel de *Pinus halepensis* (aPhal) que probablemente alivia el estrés ambiental y facilita el establecimiento de las plántulas. Como resultado del efecto de facilitación, el nicho realizado total (regeneración + adultos) de la encina se expande hacia zonas con mayor limitación ambiental.

Otro factor crítico que ha configurado la estructura y composición de los bosques mediterráneos hasta épocas muy recientes es el impacto de las actividades humanas, tal y como se ha mostrado mediante el estudio y análisis de los cambios ocurridos durante el siglo XX en la composición de los bosques de alcornoque y quejigo moruno (capítulo 3). Los datos de inventarios históricos analizados, mostraron que en pocas décadas se recuperó la cobertura vegetal en los montes del área del Parque Natural Los Alcornocales, con un incremento espectacular de la densidad de alcornoques (ver Figs. 3.2, 3.3); a la vez que se constató un descenso de la precipitación media anual y un ligero aumento de la temperatura media durante el siglo XX. Estos cambios observados en un periodo de tiempo de tan sólo un siglo son atribuibles a la gestión forestal llevada a cabo a raíz de la ordenación de los montes alcornocales (Montoya 1986). La selvicultura favoreció claramente al alcornoque como principal recurso económico para la producción de corcho (estimulando el rebrote de cepa o raíz y mediante repoblaciones) a expensas del quejigo, del que se docu-

mentaron talas selectivas en diferentes épocas, pero que no fue completamente eliminado debido a los productos secundarios que proporcionaba (carbón, leña, montanera). Por tanto, la gestión forestal ha modificado la distribución de las especies de estudio fuera del los límites establecidos por los factores ambientales (*sensu* Thomson *et al.* 1996), expandiendo el nicho realizado del alcornoque a expensas del quejigo en las zonas más húmedas y más productivas (Fig. 6.3). Estos resultados apoyan las evidencias encontradas en estudios palinológicos de que los seres humanos han inducido fuertes cambios en la composición de los bosques de *Quercus* en la Cuenca Mediterránea, en particular favoreciendo a las especies esclerófilas (Blondel y Aronson 1995; Carrión *et al.* 2000; Reille 1977).

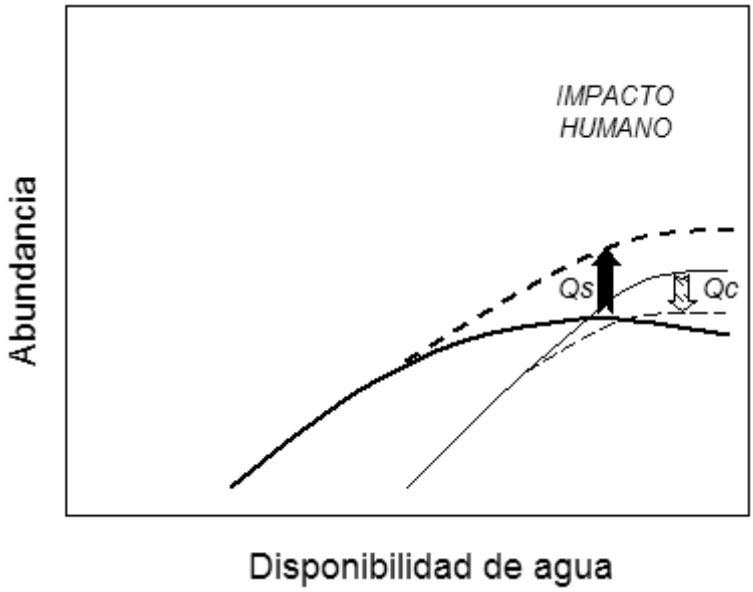

Figura 6.3 Diagrama que representa cómo la gestión forestal del último siglo ha modificado la distribución de las especies, favoreciendo al alcornoque (Qs) a expensas del quejigo moruno (Qc) en las zonas con mayor precipitación y por tanto más productivas. El tamaño y dirección de las flechas son proporcionales a la intensidad del impacto de la gestión en la abundancia de cada especie.

La huella del impacto humano se ve reflejada en la estructura actual de los bosques de alcornoque y quejigo. A escala regional se encontró que la abundancia media de las dos especies aumentaba a lo largo del gradiente de precipitación media anual, coexistiendo a partir de los 800 mm de precipitación (límite inferior para el quejigo), y con una abundancia siempre mayor de alcornoque para cualquier punto del gradiente (capítulo 3). No obstante, la estructura forestal mostró un patrón muy heterocedástico, es decir, con un incremento de la varianza, difícil de explicar sin tener en cuenta los factores de tipo local como la fisiografía del terreno o la propia historia del manejo del monte que operan a escalas espaciales menores, desde el paisaje al rodal (Fig. 6.1). Mediante el análisis realizado a escala de monte, se comprobó que el alcornoque y el quejigo mostraban una distribución diferencial en el paisaje determinada por la red de drenaje, con los quejigares claramente asociados a los hábitats más húmedos y probablemente más fértiles cercanos a los cursos

de agua (ver Fig. 3.5). En cambio, las masas de alcornocal dominaban en los rodales más alejados de los fondos de valle a mayor altitud y exposición, incluso en zonas con un mayor coste de accesibilidad, lo que pone de manifiesto que la actividad corchera se ha realizado extensamente a lo largo de toda la superficie del monte.

En los ecosistemas mediterráneos los gradientes asociados a la disponibilidad de agua son clave a la hora de explicar la distribución de las especies (Pigott y Pigott 1993; Zavala *et al.* 2000). Al comparar los rasgos entre especies esclerófilas y caducifolias, las caducifolias muestran una mayor área foliar específica (SLA, specific leaf area) y mayores tasas fotosintéticas, y por tanto un mayor crecimiento potencial que las especies esclerófilas (Reich *et al.* 1992; Antúnez *et al.* 2001; Villar *et al.* 2004). Como resultado, las caducifolias tienden a ser más abundantes en los hábitats productivos (con más nutrientes y disponibilidad de agua) por su mayor habilidad competitiva, mientras que las esclerófilas tienden a dominar en los hábitats más pobres y secos debido a su mayor eficiencia en el uso de nutrientes y mayor tolerancia a la sequía (Goldberg 1982; Aerts 1995; Corcuera *et al.* 2002). Específicamente para las especies de estudio se ha observado que bajo condiciones controladas en invernadero los tratamientos de adición de agua tuvieron efecto en parámetros fisiológicos de las especies caducifolias, con un incremento de la conductancia estomática y la tasa fotosintética de las plántulas de quejigo. Sin embargo, el efecto fue menor en las plántulas de alcornoque (ver Aranda *et al.* 2005; Pardos *et al.* 2005; Quero *et al.* 2006).

De forma similar, en el experimento de campo llevado a cabo en el capítulo 5, el aporte de agua en verano -simulando hábitats más húmedos- incrementó la supervivencia de las plántulas de quejigo, mientras que no afectó a las plántulas de alcornoque. Estos resultados sugieren que una mayor disponibilidad de agua beneficia de forma clara al quejigo. Además, Pérez-Ramos (2007) encontró valores más elevados de las tasas de asimilación neta (NARa) y de crecimiento relativo (RGRa) en condiciones limitantes de luz en las plántulas de quejigo, mientras que las plántulas de alcornoque en los sitios más sombríos obtuvieron valores negativos de asimilación neta y crecimiento relativo, indicando su menor tolerancia a la sombra. Por tanto, los diferentes rasgos morfológicos y fisiológicos del alcornoque y el quejigo pueden parcialmente explicar la distribución diferencial de las dos especies en el paisaje. Teniendo en cuenta el intenso manejo de estos bosques, parece probable que el alcornoque haya sido favorecido a lo largo de toda la superficie del monte y que los quejigares hayan sido relegados a los hábitats cercanos a los cursos de agua, más húmedos, fértiles y sombríos, donde esta especie encuentra las condiciones más favorables para su desarrollo.

Regeneración y dinámica de los bosques mixtos de alcornoque y quejigo: respuesta a la heterogeneidad a pequeña escala

La dinámica natural de los bosques mixtos de alcornoque y quejigo no se conoce con detalle y permanece incierta debido a la preocupante falta de regeneración que presentan las dos especies. El éxito de la regeneración depende del cumplimiento sucesivo de las diferentes etapas que constituyen el ciclo, de tal forma que si la probabilidad de supervivencia de una etapa a otra es próxima a cero el reclutamiento de nuevos individuos puede verse seriamente limitado o incluso colapsado (Jordano y Herrera 1995; Nakashizuka 2001). Mediante los experimentos de manipulación y siembra de semillas a lo largo de gradientes de disponibilidad de luz y de agua a pequeña escala (capítulos 4 y 5), se detectaron dos tipos de factores que limitan la regeneración natural del alcornoque y el quejigo en las fases críticas de transición entre semilla y plántula: bióticos (animales depredadores de bellotas) y abióticos (principalmente la variabilidad temporal y espacial del contenido de agua en el suelo).

En la primera fase del ciclo de regeneración estudiada se encontró que una vez que las bellotas caen al suelo por gravedad, experimentan unas tasas de remoción muy elevadas en un corto periodo de tiempo. La probabilidad de remoción tanto para las bellotas de alcornoque como para las de quejigo se incrementó a mayor cobertura vegetal, ya que la actividad de los consumidores (principalmente pequeños roedores) es mayor en las zonas de matorral (Hulme y Kunt 1999), y las bellotas más grandes fueron seleccionadas preferentemente por los ratones. Esto indica que existe un marcado patrón espacial, donde si asumimos que la mayor parte de las semillas removidas son posteriormente consumidas (Kikuzawa 1988), el reclutamiento de plántulas en las zonas con mayor cobertura vegetal se verá seriamente limitado (Acácio *et al.* 2007). Al comparar las diferencias entre especies, se comprobó que a pesar de la caída más tardía de las bellotas de alcornoque, éstas fueron removidas más rápidamente y en mayor proporción que las de quejigo en todos los casos estudiados, debido principalmente que tienen un mayor tamaño como promedio. Las diferencias entre las dos especies fueron más acusadas en años donde la producción de bellota, y por tanto la disponibilidad de recursos (bellotas) en el suelo, fue abundante. En estos casos, las tasas de remoción fueron menores para el quejigo, particularmente en las zonas con menor cobertura (abiertas), donde las bellotas de menor tamaño podrían sobrevivir y eventualmente germinar. No obstante, teniendo en cuenta que una pequeña proporción de las semillas removidas podrían no ser consumidas sino dispersadas por los roedores (Jensen y Nielsen 1986; Xiao *et al.* 2005), la regeneración del alcornoque podría verse parcialmente favorecida por dispersión secundaria debido a su preferencia respecto al quejigo.

En las siguientes fases del ciclo de regeneración, desde la germinación de bellotas hasta la supervivencia de plántulas, se detectó que las plántulas sufren a lo largo de un año un doble estrés causado por el agua: primero por exceso en la época de lluvias y posteriormente por déficit durante la sequía estival. Las abundantes lluvias que cayeron desde el otoño hasta la primavera y que caracterizan la particularidad del clima mediterráneo subhúmedo de estas sierras (ver Fig. 5.1), originaron situaciones de saturación de agua en el suelo, es decir, de encharcamiento, asociadas a las zonas sin vegetación con suelos arcillosos poco permeables; mientras que en los microhábitats con mayor cobertura vegetal, el contenido de agua en el suelo no fue tan elevado gracias a la interceptación de la lluvia por la vegetación. Es importante resaltar que, a pesar del exceso de agua que presentaron los microhábitats abiertos durante la época de lluvias, los valores de humedad del suelo alcanzados durante el período estival fueron tan bajos como en las zonas más sombrías.

El fenómeno del encharcamiento afectó negativamente a las especies de *Quercus*, disminuyendo la capacidad de germinar de las bellotas y la emergencia de las plántulas a medida que el contenido de agua en el suelo era mayor, probablemente debido a las condiciones de hipoxia que provocaba. Se constató además que en las zonas con mayor acumulación de agua en el suelo (abiertas), las plántulas emergieron más tarde, lo que redujo su posterior probabilidad de supervivencia durante el verano. El encharcamiento puede llegar a restringir las tasas de respiración y fotosíntesis, dificultando el desarrollo normal de la radícula y el tallo (Kozlowski 1984; Voesenek *et al.* 2006; Folzer *et al.* 2006). Un menor desarrollo del sistema radical puede suponer una desventaja, especialmente en ecosistemas mediterráneos, al disminuir la capacidad de la planta para absorber agua a mayor profundidad cuando ésta escasea (Nicotra *et al.* 2002). Los resultados indican que un mayor retraso en la emergencia acorta la ventana de tiempo de la época de crecimiento, e impide que las plántulas desarrollen su sistema radicular suficientemente para poder afrontar la sequía estival (Fig. 6.4). Por tanto, si persisten los eventos de precipitación en otoño e invierno pero el comienzo de la sequía se adelanta, no habrá una ventana de tiempo adecuada para que las especies desarrollen su sistema radicular y se intensificarán los problemas de regeneración forestal.

El efecto negativo de los eventos locales de encharcamiento del suelo en la regeneración forestal ha sido documentado en bosques templados sometidos a períodos intermitentes de inundación (Vincke y Delvaux 2005; Battaglia y Sharitz 2006), pero su importancia no había sido considerada hasta ahora en los ecosistemas mediterráneos. Si bien el clima de nuestra zona de estudio es particular debido a la marcada influencia oceánica, en zonas mediterráneas más continentales donde los eventos de lluvias repentinas e intensas son frecuentes, habría que explorar si este factor (el encharcamiento) puede estar limitando la regeneración de las especies arbóreas.

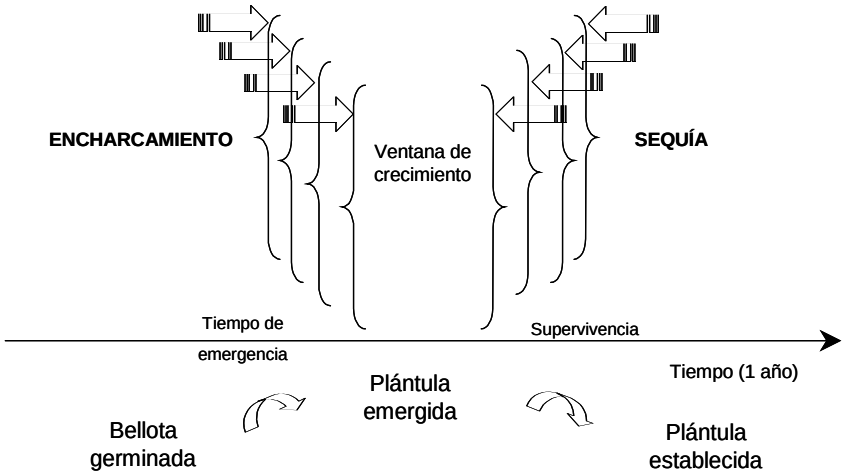

Figura 6.4 Efecto del doble estrés que causa el agua, por exceso (encharcamiento) y por déficit (sequía), en el establecimiento de plántulas de *Quercus* a lo largo de un año. Cuanto más se prolonguen en el tiempo los eventos de encharcamiento en el suelo durante la época de lluvias y más se adelante el comienzo de la sequía, menor será la ventana de tiempo que tendrán las plántulas para emerger y desarrollar un sistema radicular suficiente que les permita afrontar la sequía y sobrevivir tras el verano.

Siguiendo la metodología utilizada en los capítulos anteriores, se han explorado las diferencias entre el alcornoque y el quejigo en la probabilidad de establecimiento de plántulas a lo largo de los gradientes de luz y agua es decir, ajustando los modelos desde que las semillas fueron sembradas hasta el último censo después de un año. Se ha encontrado que la probabilidad de establecimiento de plántulas disminuye de forma exponencial a medida que la oscilación (diferencia entre el periodo húmedo y seco) del contenido de agua en el suelo es mayor (Fig. 6.5), pero no se aprecian diferencias claras entre las dos especies, que muestran una probabilidad de establecimiento similar a lo largo de todo el gradiente, aunque algo mayor para el alcornoque en el extremo más seco. Por tanto, aparentemente el alcornoque y el quejigo no difieren en su respuesta global al efecto del agua en el suelo, y muestran un patrón similar: el establecimiento de plántulas se ve seriamente limitado en las zonas que acumulan mayor cantidad de agua en el suelo en la época de lluvias y se secan en la época estival.

No obstante, tal y como se ha mostrado en el capítulo 5, al analizar la respuesta de las especies en cada fase por separado (germinación, emergencia y supervivencia), se ha encontrado que las especies difirieren en los picos de mortalidad entre fases. El quejigo experimentó unas tasas de germinación más bajas que el alcornoque a lo largo de todo el gradiente de agua en el suelo, que parecen intrínsecas a la especie ya que también se observaron en condiciones de laboratorio (Pérez-Ramos 2007). Sin embargo, su emergencia fue mayor y más temprana, lo que determinó su mayor supervivencia tras el verano, especialmente en aquellas plántulas que emergieron más temprano y recibieron un aporte extra de agua. Por el contrario, las bellotas de alcornoque mostraron una mayor capacidad de germinación que las de quejigo para cualquier nivel de contenido de agua en el suelo; pero su emergencia fue algo menor y más tardía, lo que provocó una mayor mortalidad de las plántulas durante el verano. El tamaño de semilla también jugó un papel importante en el establecimiento de plántulas, tal y como ha sido argumentado en otros estudios (p.ej., Bonfil 1998; Poorter y Rose 2005). Un mayor tamaño de semilla tuvo un efecto positivo en la germinación y emergencia del alcornoque, mientras que para el quejigo este efecto no fue tan determinante, e incluso fue negativo para su emergencia.

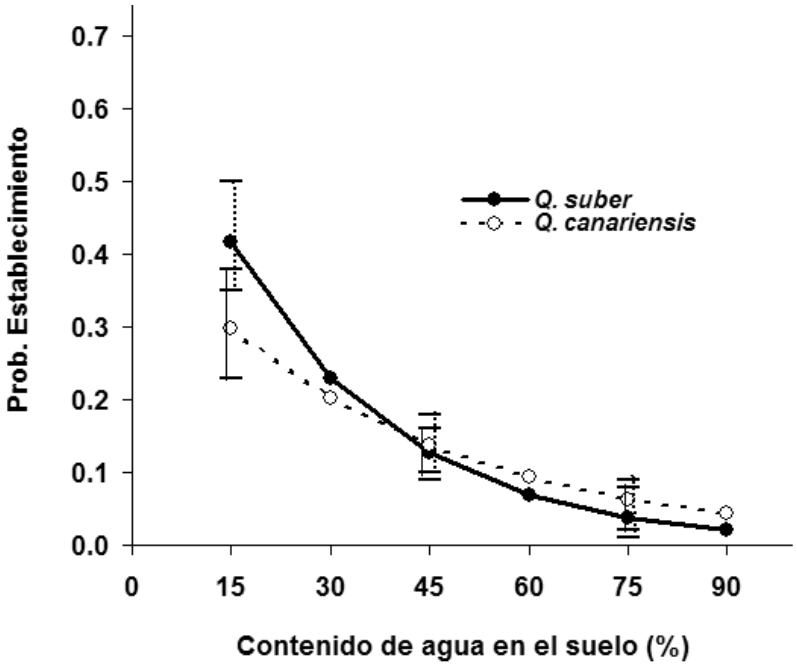

Figura 6.5 La probabilidad de establecimiento de las plántulas de alcornoque y de quejigo disminuye exponencialmente a lo largo del gradiente de oscilación de agua en el suelo (calculado como la diferencia entre el contenido de agua en la época de lluvias y en la época seca). El establecimiento de plántulas es prácticamente nulo en las zonas que experimentan mayor oscilación (encharcamiento-sequía). Las dos especies muestran una respuesta similar, aunque la probabilidad de establecimiento del alcornoque es algo mayor que la del quejigo en el extremo más seco del gradiente.

Teniendo en cuenta las diferencias interespecíficas encontradas entre las fases de establecimiento de plántulas, así como la fenología de las especies, cabría encontrar patrones diferenciales de reclutamiento entre el alcornoque y el quejigo en función de la variación interanual de las precipitaciones, que podrían favorecer la coexistencia de las dos especies. A pesar de que es necesario tener cautela a la hora de extrapolar los resultados de un experimento de un año, el amplio gradiente de agua en el suelo capturado nos permite lanzar algunas hipótesis sobre lo que ocurriría en la dinámica de la regeneración de las dos especies bajo diferentes escenarios. Durante inviernos no muy lluviosos, sin encharcamiento, el alcornoque se beneficiaría respecto al quejigo por sus mayores tasas de germinación y emergencia bajo condiciones de suelo húmedo pero bien drenado. Sin embargo, ante lluvias intensas de otoño e invierno, el alcornoque experimentaría un mayor retraso en su emergencia (por su caída de la bellota más tardía y su menor tolerancia al encharcamiento) que resultaría en un menor reclutamiento de esta especie. Por otra parte, las lluvias tardías de primavera y en especial las esporádicas de verano parecen favorecer al quejigo. De forma global, una reducción general en las precipitaciones y el aumento de la temperatura, como está previsto en el actual proceso de cambio climático, perjudicará a las dos especies.

Modelo integrado de regeneración

Al comparar todas las etapas del ciclo de regeneración estudiadas, parece existir un conflicto entre las fases demográficas (*sensu* Schupp 1995), donde los microhábitats con menor riesgo de depredación para las semillas son los menos favorables para el subsiguiente establecimiento de plántulas y viceversa. De esta forma, la probabilidad de las bellotas de escapar de los depredadores es mayor en las zonas abiertas, pero es precisamente en estas zonas donde las condiciones para el establecimiento de plántulas son menos favorables debido al efecto de los episodios de encharcamiento y sequía en el suelo. Asimismo, la influencia del tamaño de la bellota en cada fase es opuesta, es decir, las bellotas más pequeñas tienen mayor probabilidad de sobrevivir a la acción de los depredadores, pero a su vez son las que menor probabilidad de germinación y emergencia presentan (ver Gómez 2004).

Dados estos resultados, cabe preguntarse qué ocurre de forma global en ambas especies si integramos todas las fases del ciclo estudiadas, desde que las bellotas caen al suelo y sobreviven a la acción de los depredadores hasta el establecimiento de plántulas de un año. Es decir, ¿difieren el alcornoque y el quejigo en la probabilidad de reclutamiento acumulada en función de los dos factores principales encontrados, la cobertura vegetal y el tamaño de semilla? Para comprobarlo, se han expresado las ecuaciones de cada fase del ciclo en función del peso de la semilla y el índice de área foliar (LAI). Para el modelo de remoción de bellotas se ha tomado la ecuación del año en que la producción de bellotas fue escasa, por la que es razonable asumir que todas las bellotas removidas fueron posteriormente consumidas, y por tanto no sobrevivirán a la siguiente fase. En las fases de germinación, emergencia y supervivencia de plántulas se han tomado los modelos que incluían el contenido de agua en el suelo y el tamaño de la semilla. Posteriormente, en estas ecuaciones el contenido de agua en el suelo (SVWC) ha sustituido por la expresión que lo relaciona con el gradiente de luz, donde LAI = 65,05 - 10,10 x SVWC.

El resultado de multiplicar las probabilidades de transición entre las fases a lo largo de los gradientes de luz y peso de la bellota se muestran en la Figura 6.6. La combinación de zonas con poca cobertura vegetal y las plántulas de bellotas de menor tamaño parece la más favorable para el reclutamiento efectivo de plántulas de las dos especies. Prácticamente a lo largo de todo el gradiente de cobertura vegetal el alcornoque presenta una probabilidad de reclutamiento nula para

cualquier tamaño de bellota; tan solo en las zonas abiertas las plántulas de bellotas de menor tamaño podrían llegar a establecerse con una probabilidad media de 0,02. El quejigo muestra una probabilidad de reclutamiento mayor (~ 0,05) que el alcornoque en estas zonas.

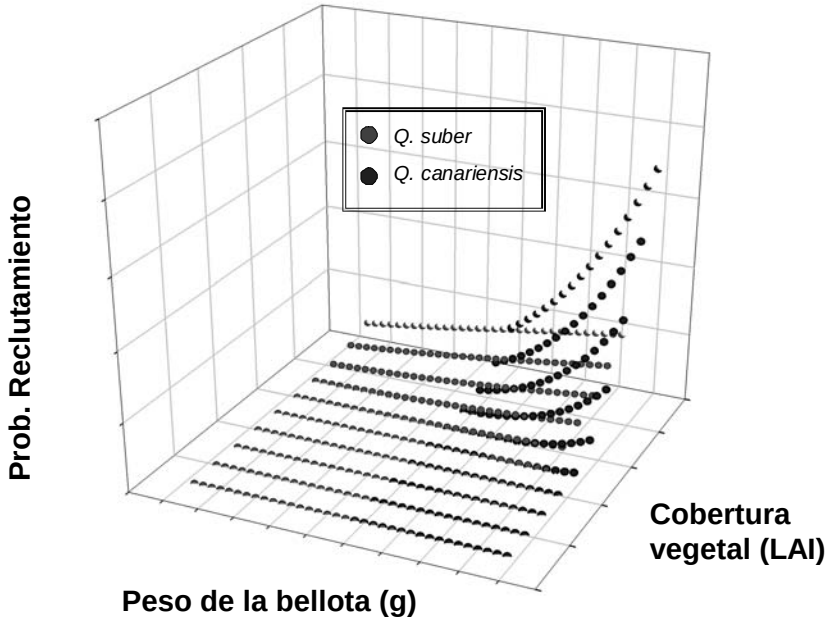

Figura 6.6 Probabilidad de reclutamiento acumulada para el alcornoque y el quejigo, calculada como el producto de las probabilidades de supervivencia de las fases de depredación y establecimiento de plántulas en función del gradiente de cobertura vegetal y el peso de la bellota. El reclutamiento de las dos especies es prácticamente nulo en las zonas con mayor cobertura vegetal. Tan sólo en las zonas más abiertas una pequeña proporción de plántulas con semillas más pequeñas lograrían sobrevivir, siendo la probabilidad media para el quejigo mayor que para el alcornoque.

En conclusión, teniendo en cuenta que la limitación del reclutamiento y la falta de regeneración es mayor para el alcornoque (Montero 1987; Cueto 2000; Ajbilou *et al.* 2006), que la producción de corcho está disminuyendo debido al envejecimiento de las masas de alcornocal (Torres *et al.* 1994; Torres 1995), y que la presión sobre el quejigo ha cesado en las últimas décadas gracias a las recientes políticas de conservación y gestión forestal que lo protegen como especie de Interés Especial (Ley de la Flora y la Fauna silvestres, BOJA 12/11/2003; Anónimo 2004), cabe esperar una tendencia a la recuperación de los quejigares localmente en aquellas zonas más húmedas donde esta especie ha sido desplazada por la acción humana.

Perspectivas de investigación: escalando los patrones de regeneración a la estructura forestal en el paisaje

Las predicciones de cambio en la estructura de las masas mixtas y la toma de decisiones a la hora de elaborar los planes de restauración forestal no pueden basarse únicamente en la extrapolación de los patrones vegetación-ambiente que observamos en la actualidad, ya que estos bosques han sido sometidos a una fuerte transformación antrópica. Investigar cómo interaccionan la fenología de las especies, la producción de semillas, la abundancia de depredadores, la estructura del hábitat y la variabilidad en las precipitaciones parecen clave para comprender los patrones de regeneración de los bosques de alcornoque y quejigo y dilucidar parcialmente la dinámica de estos bosques.

Las futuras líneas de investigación que darán continuidad a los resultados obtenidos en esta Tesis Doctoral, van a centrarse en el desarrollo de modelos dinámicos de la regeneración del alcornoque y del quejigo a partir de las funciones de respuesta de las dos especies a la heterogeneidad ambiental a pequeña escala obtenidas de la parametrización de los datos experimentales presentados en los capítulos 4 y 5. En concreto, el objetivo será concatenar las diferentes fases del ciclo de regeneración de las dos especies e incluir la variabilidad interanual en la producción de frutos y la dispersión, para simular el reclutamiento de nuevos individuos en el paisaje bajo diferentes escenarios de duración e intensidad de las precipitaciones. Estos modelos podrán ayudar a resolver las incertidumbres que existen en cuanto a la regeneración y dinámica de los bosques mixtos de alcornoque y quejigo ante los posibles efectos del cambio climático y se pretende que sirvan como herramientas de decisión en los programas de restauración forestal.

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Capítulo 7

Capítulo 7

Conclusiones

1. Factores de tipo climático y edáfico explicaron la distribución diferencial de las especies de pinos y robles en Andalucía. El gradiente térmico determinó principalmente la distribución de los pinos, mostrando la siguiente secuencia de especies desde las zonas más frías a las más cálidas: *Pinus sylvestris*, *P. nigra*, *P. halepensis*, *P. pinaster*, y *P. pinea*. La distribución de los robles apareció asociada a un gradiente de disponibilidad hídrica, con *Quercus suber* y *Q. canariensis* coexistiendo en las zonas más húmedas, seguidas de *Q. faginea* y *Q. pyrenaica*. Hacia zonas más áridas se encontró *Q. ilex*, que mostró la mayor amplitud de nicho. El contenido de calcio en el suelo fue clave para *P. halepensis*, asociado a suelos básicos, mientras que *Q. suber* y *Q. canariensis* aparecieron asociados a suelos ácidos.

2. Se detectó una escasa regeneración en los bosques de las especies de *Pinus* y *Quercus*, cuya abundancia varió a lo largo de los gradientes ambientales y en función del tipo de hábitat. El porcentaje de las parcelas del Segundo Inventario Forestal Nacional sin regenerado fue de alrededor de un 45% para las especies de *Pinus*, mientras que varió entre un 20% y un 60% en los rodales de *Quercus*, alcanzando los valores más altos para el alcornoque (*Q. suber*) y el quejigo moruno (*Q. canariensis*). La regeneración de las especies de *Pinus* se observó bajo el propio dosel de los pinares y de forma importante en zonas forestales sin cobertura arbórea, reflejando su capacidad colonizadora; mientras que la regeneración de los *Quercus* se encontró asociada a la cobertura del dosel arbóreo.

3. En algunas especies como la encina (*Q. ilex*) y el quejigo (*Q. faginea*), la distribución del regenerado a lo largo de los gradientes ambientales fue diferente que para los adultos. La regeneración de estas dos especies era más abundante bajo los pinares que bajo el dosel de su misma especie, particularmente en las zonas más frías y áridas donde no se desarrollaban quejigares ni encinares. Las especies de *Pinus* pueden estar ejerciendo un efecto de facilitación en el establecimiento de los *Quercus*, permitiendo la expansión parcial de sus nichos hacia zonas con mayor limitación ambiental.

4. El impacto de las actividades humanas ha configurado la estructura de los bosques mediterráneos hasta épocas muy recientes. El análisis de los inventarios históricos de los montes públicos del Parque Natural Los Alcornocales ha mostrado que en tan sólo un siglo el manejo forestal ha modificado fuertemente la composición de los bosques mixtos de alcornoque y quejigo moruno. La selvicultura ha favorecido al alcornoque para la producción de corcho como principal recurso económico, en detrimento del quejigo y otras especies, especialmente en las zonas con mayor régimen de precipitaciones y por tanto más productivas.

5. La huella del impacto humano se ve reflejada en la estructura actual de los bosques de alcornoque y quejigo. A escala regional se encontró que las dos especies coexisten a partir de los 800 mm de precipitación media anual, siendo la abundancia media de alcornoque siempre mayor para cualquier punto del gradiente. Sin embargo, al reducir la escala de análisis al paisaje se observó que las dos especies presentan una distribución diferencial determinada por la red de drenaje. Los quejigares están claramente asociados a los hábitats más húmedos cercanos a los cursos de agua, mientras que la abundancia de alcornoque es mayor a medida que aumenta la distancia a los fondos de valle, incluso en las zonas con mayor coste de accesibilidad para la extracción de corcho.

6. La regeneración de alcornoque y de quejigo se ve seriamente limitada por la acción de los animales consumidores de bellotas, sobre todo si la producción de frutos del año es baja, ya que la disponibilidad de recursos (bellotas) en el suelo escasea. En ambas especies la probabilidad de remoción de bellotas se incrementó con la cobertura vegetal, donde la actividad de los pequeños roedores es mayor. Las bellotas más grandes fueron seleccionadas preferentemente por los ratones. A pesar de la caída más tardía de las bellotas de alcornoque, éstas fueron removidas más rápidamente y en mayor proporción que las de quejigo, posiblemente debido a que tienen mayor tamaño como promedio.

7. Durante el establecimiento de plántulas, el contenido de agua en el suelo actúa como un doble factor limitante de la regeneración de los *Quercus*: por exceso en la época de lluvias y por déficit durante el verano. Los episodios temporales de encharcamiento del suelo, asociados a los microhábitats con poca cobertura vegetal, resultaron en una disminución de la probabilidad de germinación y emergencia de plántulas. Asimismo, provocaron un retraso en la emergencia de las plántulas, lo cual redujo su posterior probabilidad de supervivencia durante el verano.

8. La probabilidad de establecimiento de plántulas de alcornoque y de quejigo disminuyó de forma similar a lo largo del gradiente de oscilación de agua en el suelo, pero las especies mostraron diferencias en cada fase demográfica estudiada. Así, la tasa más baja de germinación del quejigo en comparación con el alcornoque, se vio compensada por su mayor éxito en la emergencia, que fue más temprana y determinó su mayor supervivencia tras el verano. Además la adición de agua durante el periodo estival redujo la mortalidad de plántulas de quejigo, mientras que las de alcornoque no respondieron al tratamiento de riego.

9. Se encontró un conflicto entre las fases demográficas estudiadas. Los microhábitats con menor riesgo de depredación para las semillas (aquéllos con menor cobertura vegetal) fueron los menos favorables para el establecimiento de las plántulas. Asimismo, la influencia del tamaño de la bellota en cada fase fue opuesta; mientras las bellotas más pequeñas mostraron mayor probabilidad de sobrevivir a la acción de los depredadores, a su vez fueron las que menor probabilidad de germinación y emergencia presentaron.

10. La variabilidad interanual de las precipitaciones puede favorecer la coexistencia de las dos especies. Durante inviernos no muy lluviosos, sin encharcamiento, el alcornoque se beneficiaría respecto al quejigo por sus mayores tasas de germinación y emergencia bajo condiciones de suelo húmedo pero bien drenado. Sin embargo, ante lluvias intensas de otoño e invierno, el alcornoque experimentaría un mayor retraso en su emergencia que resultaría en un menor reclutamiento de esta especie. Por otra parte, las lluvias tardías de primavera y en especial las esporádicas de verano parecen favorecer al quejigo. De forma global, una reducción general en las precipitaciones y el aumento de la temperatura, como está previsto en el actual proceso de cambio climático, perjudicará a las dos especies.

11. Dado que la presión sobre el quejigo ha cesado en las últimas décadas y que las actuales políticas de conservación y gestión forestal lo protegen, cabría esperar una tendencia a la recuperación de los quejigares localmente en aquellas zonas donde esta especie ha sido desplazada por la acción humana.

12. La aproximación multi-escala nos ha permitido detectar las principales tendencias de variación en la distribución de las especies forestales. Mediante el análisis histórico de los inventarios hemos comprobado la importancia de la gestión en los cambios recientes de la estructura y composición de los bosques. El estudio de los procesos de regeneración a escala de rodal y de microhábitat, combinado con las técnicas de modelización, nos permite establecer las relaciones entre las condiciones del medio y las probabilidades de éxito en las distintas fases de regeneración. La complejidad de la dinámica forestal requiere esta combinación de técnicas y de escalas de investigación.